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Karyotypes and Evolution of the *spinosus* Group of Lizards in the Genus *Sceloporus*[1]

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INTRODUCTION

The lizard genus *Sceloporus* provides excellent opportunities for investigations in evolutionary biology. This genus, which contains nearly 60 species and twice as many subspecies, is one of the largest in the family Iguanidae and one of the largest lizard genera in the New World. Moreover, the various species of *Sceloporus* exhibit a spectrum of morphological, ecological, and physiological adaptations to a variety of habitats and microhabitats geographically distributed from southern Canada through most of the vast territory of the continental United States, Mexico, and Central America to western Panama.

With few exceptions, such as Smith's (1939) monographic treatment of the taxonomy of essentially the entire genus and Etheridge's (1964) consideration of osteological details in a large number of species, the potential provided by *Sceloporus* has not been exploited. As is the case with most genera of reptiles, the cytogenetics of *Sceloporus* has hardly been touched.

Painter (1921) first considered *Sceloporus* chromosomes, and reported

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generalities on two species (in addition to other species in different genera). His and other early investigations of reptilian karyotypes generally were hampered and partly inaccurate due to the lack of proper techniques and equipment. These problems are now greatly reduced, and recent investigations indicate the potential of cytogenetics for effectively analyzing *Sceloporus* systematics (Lowe, Wright, and Cole, 1966; Cole, Lowe, and Wright, 1967; Lowe, Cole, and Patton, 1967; Cole and Lowe, 1968).

The present paper considers the cytogenetics of lizards in the *spinosus* group, which is one of the 15 species groups recognized as comprising the genus *Sceloporus* (Smith, 1939). The *spinosus* group includes nine species: *Sceloporus clarki* Baird and Girard, *S. melanorhinus* Bocourt, *S. orcutti* Stejneger, *S. magister* Hallowell, *S. lundelli* Smith, *S. edwardtaylori* Smith, *S. olivaceus* Smith, *S. spinosus* Wiegmann, and *S. horridus* Wiegmann (Smith, 1939; Smith and Taylor, 1950). These nine species (27 species and subspecies) make the *spinosus* group one of the largest and most diverse in the genus; it ranges from Guatemala northward to Nevada and Utah (Smith and Taylor, 1966; Shannon and Urbano, 1954; Phelan and Brattstrom, 1955; Tanner, 1955; Hardy and McDiarmid, 1969). Species within this group occupy various habitats ranging from the ancient Neotropical forests in southern Mexico and northern Central America to the relatively recently derived deserts of North America. Furthermore, the species group includes those forms that are primarily arboreal as well as those that are primarily ground-dwelling. Thus this group constitutes a unit particularly suitable for evolutionary investigations.

The karyotype analyses reported herein reveal examples of the following cytogenetic phenomena within the nine species of the *spinosus* group: interspecific and intraspecific variation in chromosome number and morphology; polymorphism in local populations; cytologically recognizable sex chromosomes; and natural chromosomal aberrations.

METHODS

The present report is based on the examination of chromosomes in approximately 2200 cells from 159 lizards (88 males, 71 females) representing all nine species comprising the *spinosus* group. Chromosomes from bone marrow and testicular tissues were prepared for microscopic examination by means of the colchicine, hypotonic citrate, air-dried procedures used by Patton (1967), with slight modifications for lizards (Lowe, Wright, and Cole, 1966).

The terminology used in reference to chromosome shapes is similar to that employed by Lowe and Wright (1966) for *Cnemidophorus*. A metacentric chromosome has a median or essentially median centromere;

a telocentric chromosome has a terminal or essentially terminal centromere; a submetacentric chromosome has the clearly non-median centromere closer to the middle than to either end; and a subtelocentric chromosome has the clearly non-terminal centromere closer to one end than to the middle.

I was fortunate enough to acquire field experience with each of the species in the group while collecting individuals for karyotypic analysis. Each lizard examined was preserved, and its sex was determined by dissection. All specimens are in the herpetological collection of the Department of Biological Sciences at the University of Arizona (U.A.Z.; see Specimens Examined, below).

KARYOTYPES

Sceloporus clarki

The karyotype of Clark's spiny lizard was previously described by Lowe, Cole, and Patton (1967), who examined chromosomes in detail in 106 mitotic cells from 11 individuals (seven males, four females) from localities covering more than the northern half of the geographic range of the species in Mexico and the United States. The karyotype appeared monomorphic; as is considered typical for most species of lizards, neither sex-correlated chromosomes nor geographic differences in the karyotype were apparent.

More extensive field and laboratory investigations, however, involving analysis of more than 1200 cells from 81 individuals (46 males, 35 females), revealed that in addition to the typical karyotype previously described, there are at least two similar, but clearly distinct and considerably rarer atypical karyotypes. The three karyotypes (fig. 1) are described immediately below, referred to as KA, KB, and KC.

KARYOTYPE KA: The typical karyotype of *S. clarki* has a diploid number of 40 chromosomes ($2n = 40$). These include 20 macrochromosomes (10 homomorphic pairs) and 20 microchromosomes (apparently 10 homomorphic pairs; fig. 1A). The pairs are numbered in order of decreasing length for the purpose of describing the karyotype. Of the macrochromosomes, numbers 1 and 7 are submetacentric and number 1 bears a terminal satellite on the long arm; the satellites, although consistently situated here, are not conspicuous in many cells. The remaining macrochromosomes are telocentric and several are difficult or impossible to differentiate individually because of their general similarities in size and shape; numbers 4, 5, and 6 are in most cases particularly difficult to differentiate, as are numbers 8, 9, and 10. Morphology of the microchromosomes usually is difficult to determine, particularly in this species,

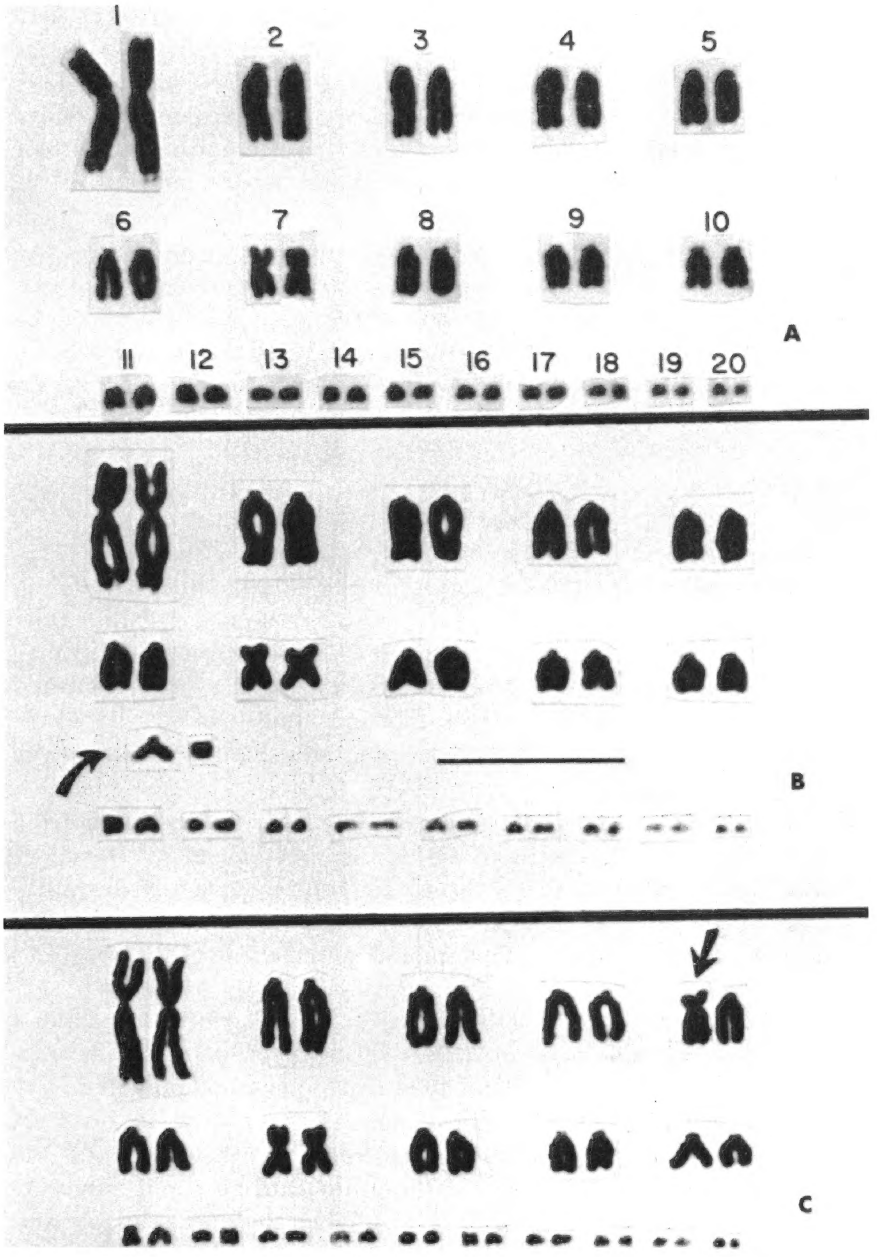

FIG. 1. Chromosomes of three specimens of *Sceloporus clarki* ($2n = 40$) from southern Arizona. A. Karyotype KA, described on pages 3–5; U.A.Z. No. 25464, female. B. Karyotype KB, described on pages 5–7; arrow indicates heteromorphic pair; line represents 10 μ; U.A.Z. No. 24186, female. C. Karyotype KC, described on pages 7–9; arrow indicates heteromorphic pair; U.A.Z. No. 24904, male.

and cannot be considered definite because of their minute dimensions; nevertheless, in many cells it appears that number 12 and another pair (*ca.* number 14) are subtelocentric whereas the rest are telocentric. Most of the microchromosomes cannot be individually differentiated with confidence in all cells examined.

KARYOTYPE KB: This atypical karyotype (fig. 1B) is similar to the typical KA. The 20 macrochromosomes are the same as those in KA; the remaining 20 chromosomes consist of 19 apparently typical microchromosomes plus a single telocentric chromosome that is intermediate in size between the smallest macrochromosomes and the largest microchromosomes ($2n = 40$). This karyotype occasionally is abbreviated hereafter as $20+1+19$ (the typical karyotype being represented by $20+0+20$ chromosomes). In mitotic cells containing the $20+1+19$ karyotype it appears as though the intermediate-sized element and one of the microchromosomes may be unpaired. Analysis of meiotic cells, however, revealed that these two "odd" chromosomes constitute a heteromorphic pair (figs. 1B, 2).

Examination of testicular tissue revealed that spermatogonia have the same karyotype as bone marrow cells. Furthermore, during meiosis I in primary spermatocytes (fig. 2A), there are regularly formed 10 bivalents of macrochromosomes, one intermediate-sized bivalent, and 9 bivalents of microchromosomes ($10+1+9$). The intermediate bivalent is composed of the single intermediate-sized chromosome and the "unpaired" microchromosome, which, therefore, clearly constitute a heteromorphic pair (size heteromorphism).

Analysis of 51 cells at prophase II and metaphase II (secondary spermatocytes) revealed normal chromosome segregation from the heteromorphic bivalent in anaphase I, as both expected types of secondary spermatocytes ($10+1+9$ and $10+0+10$; fig. 2B, C) occur in a frequency not significantly different from the hypothetical 1:1 ($N = 20$ cells having $10+1+9$; $N = 31$ cells having $10+0+10$; $\chi^2 = 2.38$; $0.20 > P > 0.10$). As meiosis proceeds normally, it is reasonable to assume that both types of spermatozoa are generated in equal frequency.

Difficulty in analyzing the minute microchromosomes precludes designating precisely which pair is heteromorphic. It appears to be one of the larger pairs, but not the largest; I suggest that it is *ca.* number 12 (fig. 1B).

The mode of origin of the heteromorphic condition is uncertain, although a reasonable explanation is available. Reciprocal translocation is unlikely because no polyvalents are formed in meiosis I; the intermediate-sized bivalent is regularly formed ($N = 45$ cells examined at

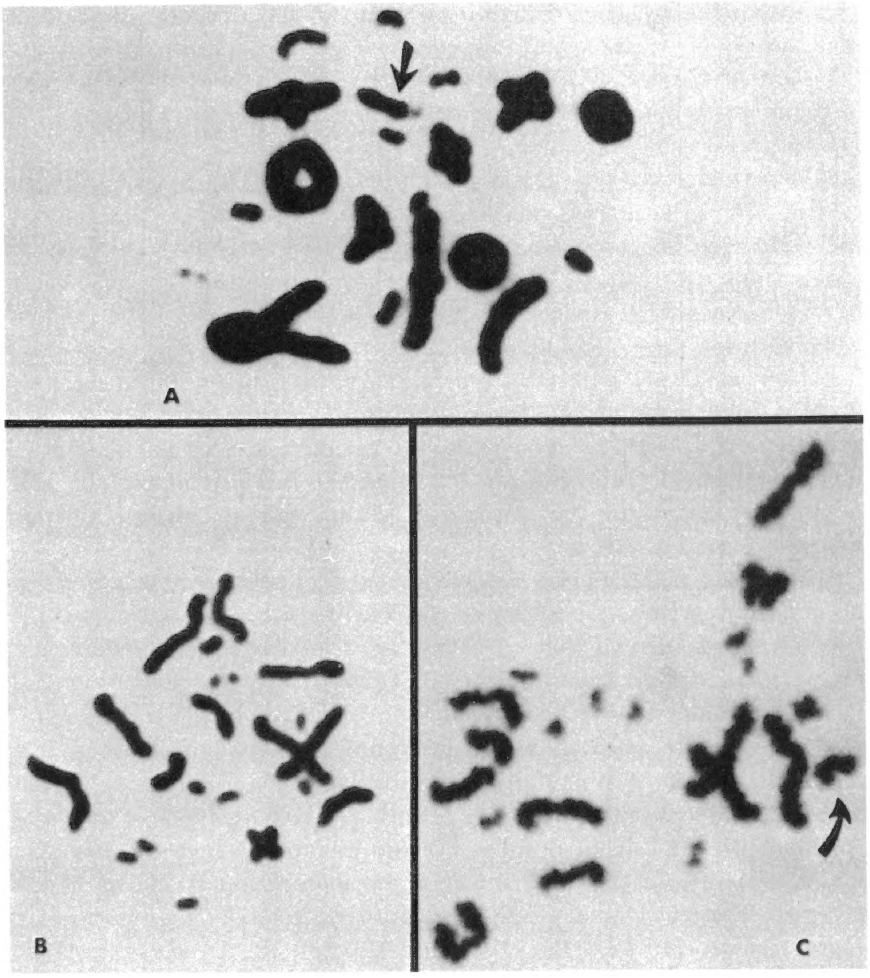

FIG. 2. Spermatocytes from an individual of *Sceloporus clarki* with atypical 20 + 1 + 19 karyotype (KB); all cells from U.A.Z. No. 24862, male from same locality as those illustrated in figure 1. A. Primary spermatocyte (metaphase I), with 10 bivalents of macrochromosomes + one intermediate-sized bivalent (arrow) + nine bivalents of microchromosomes ($n = 20$). Intermediate bivalent represents heteromorphic pair (arrow). B. Secondary spermatocyte (metaphase II), with 10 + 0 + 10 constitution ($n = 20$). C. Secondary spermatocyte (metaphase II), with 10 + 1 + 9 constitution ($n = 20$). Arrow indicates the intermediate-sized chromosome.

diakinesis and metaphase I). This suggests an origin involving duplication or deletion, but it remains uncertain whether the large member of

the pair represents the derived condition (duplication or addition of chromatin) or whether the smaller member is derived (deletion or loss of chromatin). Presumably a diploid bisexual species such as *S. clarki* is more likely to withstand addition of chromatin rather than loss of chromatin, so I suggest that the larger member of the heteromorphic pair is derived. Such enlargement could result, for example, following crossover between two homologous chromosomes that differ from the standard gene arrangement by two overlapping inversions (one each); a single crossover within the common inverted segment would produce an enlarged chromosome bearing a duplicated segment and no deletions, which may survive, plus a shortened chromosome with deletions, which may not survive.

Thus it appears that the only difference between the typical karyotype KA (20+0+20) and KB (20+1+19) is that in the latter, an individual "microchromosome" is now considerably larger than its homologue (a true microchromosome; fig. 1A, B). This karyotype is not sex correlated (see below), as it is equally expressed in lizards of both sexes from the same locality.

KARYOTYPE KC: This atypical karyotype (fig. 1C) is also similar to the typical one (KA) and differs from it in having one heteromorphic pair of chromosomes. In this case, both members of the heteromorphic pair are the same size, but one is subtelocentric and one is telocentric. Because of the similarities of the telocentric chromosomes in pairs 4 through 6 in the typical karyotype, I cannot be certain as to precisely which pair is heteromorphic; it is approximately number 5 (fig. 1C). Again, there is no sex correlation.

As with the first heteromorphic karyotype considered (KB), KC also is expressed equally in spermatogonia and bone marrow cells. At metaphase I in primary spermatocytes (fig. 3A), 10 bivalents of macrochromosomes and 10 of microchromosomes (10+0+10) regularly form. These bivalents and the absence of polyvalents (N = 27 cells examined at diakinesis and metaphase I) clearly reveal that the chromosomes in question constitute a heteromorphic pair (shape heteromorphism).

Analysis of 100 secondary spermatocytes at prophase II and metaphase II (fig. 3B, C) revealed normal chromosome segregation from the heteromorphic bivalent in anaphase I, as both expected types of secondary spermatocytes (one with the atypical subtelocentric number 5 and one with the typical telocentric number 5) occur in a frequency not significantly different from the hypothetical 1:1 (N = 59 cells having the subtelocentric number 5; N = 41 cells having the telocentric number 5; $\chi^2 = 3.24$; $0.10 > P > 0.05$). Thus, as meiosis proceeds normally, it is

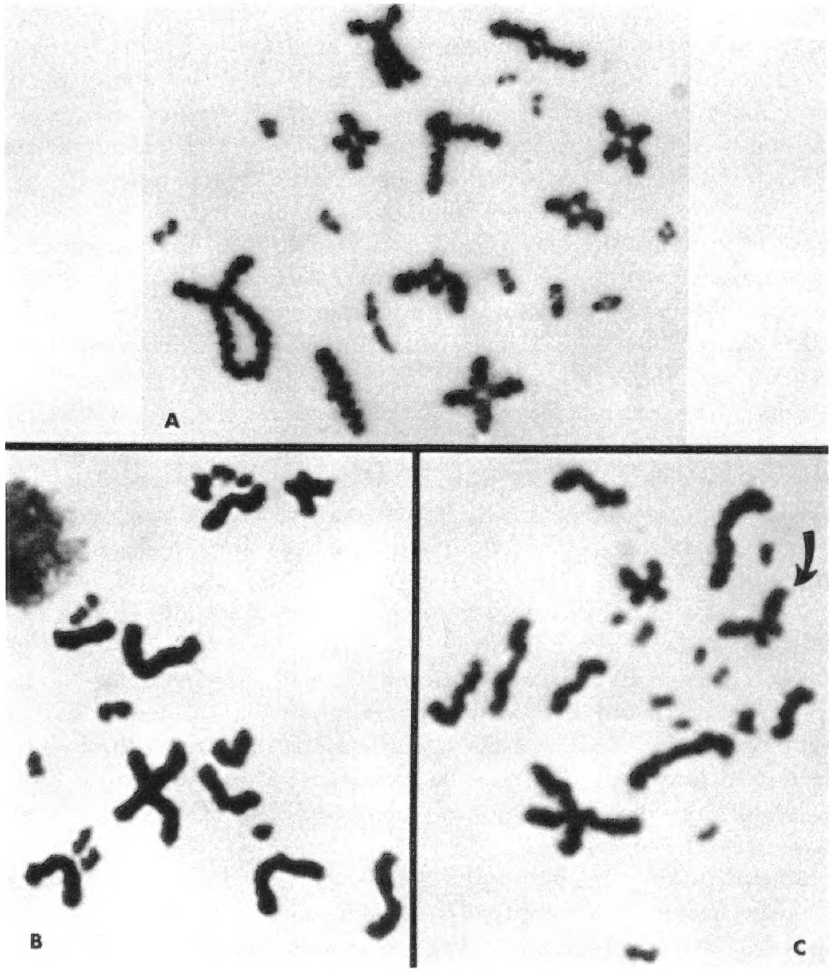

FIG. 3. Spermatocytes from an individual of *Sceloporus clarki* having atypical karyotype with subtelocentric macrochromosome (KC); all cells are from U.A.Z. No. 24904, male (fig. 1 C). A. Primary spermatocyte (diakinesis), with 10 bivalents of macrochromosomes + 10 of microchromosomes ($n = 20$). B. Secondary spermatocyte (metaphase II), with 10 + 0 + 10 constitution ($n = 20$), and macrochromosomes represented by typical complement of eight telocentric elements and two submetacentric elements. C. Secondary spermatocyte (metaphase II), with 10 + 0 + 10 constitution ($n = 20$), and macrochromosomes represented by atypical complement of seven telocentric elements, one subtelocentric element [atypical *ca.* no. 5 (arrow)] and two submetacentric elements.

reasonable to assume that both types of spermatozoa are produced in equal frequency.

This heteromorphism presumably resulted from either an unequal pericentric inversion or a centromere shift (centric shift); inversion is more probable because it requires fewer breaks (two instead of three). I suspect that the telocentric condition is ancestral because it abounds throughout the range of the species (this heteromorphism is known rarely from only one locality; see below) and particularly as *S. melanorhinus,* a species considered more primitive than *S. clarki,* possesses the same telocentric chromosome but not the subtelocentric one (see below).

DISTRIBUTION AND FREQUENCY: The typical karyotype (KA) of *S. clarki* occurs abundantly in individuals of both sexes obtained at numerous localities extending from Arizona and New Mexico southward through Sinaloa. The atypical karyotype having 20 + 1 + 19 chromosomes (KB) is presently known from only two localities: (1) 6 miles northwest of La Concha, 29 miles (by Mex. 15) southeast of Escuinapa, Sinaloa, Mexico, and (2) the Patagonia Mountains and Pajarito Mountains, Santa Cruz County, Arizona (these last populations are continuous throughout the vicinity of Nogales or a bit south of it, and thus specimens from both mountains are treated as one population sample). The atypical karyotype with the heteromorphic pair of macrochromosomes (KC) is presently known only from the locality in southern Arizona.

A sample of 51 lizards from the southern Arizona locality was examined in order to estimate the local frequencies of the three karyotypes. Of these 51 individuals (29 males, 22 females), 34 (23 males, 11 females; 66.66667 per cent) had the typical 20 + 0 + 20 karyotype (KA), 13 (4 males, 9 females; 25.49020 per cent) had the atypical 20 + 1 + 19 karyotype (KB), and 4 (2 males, 2 females; 7.84314 per cent) had the atypical karyotype with a subtelocentric number 5 chromosome (KC). A chi-square test for homogeneity using a 2 by 3 contingency table (see Simpson, Roe, and Lewontin, 1960) indicates that there is no difference in the frequency distributions of these karyotypes in the two sexes ($\chi^2 = 5.296$; $0.10 > P > 0.05$); that is, occurrence of these heteromorphic pairs of chromosomes is not sex correlated.

It has been discussed and commented on above that (1) all three of the known karyotypes of *S. clarki* occur together at one locality (southern Arizona), (2) individual males with either of the two heteromorphic pairs of chromosomes carry on normal meiosis, and in each case generate equal numbers of both types of spermatozoa, (3) the karyotypes occur in equal frequencies in both sexes, and (4) the frequencies are as follows: (A) the typical karyotype = 0.6666667, (B) the 20 + 1 + 19 karyotype = 0.2549020, and (C) the karyotype with a subtelocentric number 5 macrochromosome = 0.0784314. From this information, it

follows that six additional karyotypes of *S. clarki* theoretically occur at the same locality: two are the homozygotes of each of the rarer atypical chromosomes thus far known only as heterozygotes, and four are the various possible combinations of both. Apparently these occur in extremely low frequencies, assuming, of course, that they do indeed occur and that their existence is not obviated by particular combinations of lethal or sterility-inducing genes.

The Hardy-Weinberg formula and chi-square analysis were employed to determine whether the observed frequencies of the karyotypes differed significantly from what could be expected if the three karyotypes in southern Arizona occurred at an equilibrium. The expected frequency of each karyotype at equilibrium was estimated from its observed frequency in the population sample at hand. All calculations were carried out to seven decimal places in order to accommodate the very low theoretical frequencies at which some of the rarer karyotypes may exist.

At first, as the atypical karyotypes (KB and KC) each varied from the typical one (KA) with respect to different pairs of chromosomes (*ca.* number 12 and *ca.* number 5, respectively), each atypical chromosome was analyzed independently. In each case, three karyotypic conditions were theoretically possible: (1) homozygous typical, (2) heterozygous, and (3) homozygous atypical; and in each case only the first two were observed. Thus each case was individually treated in the manner of a Hardy-Weinberg problem involving one locus and two alleles. For the *ca.* number 12 chromosomes (as in karyotype KB), chi-square analysis revealed no significant difference between the frequencies observed in the population sample and the hypothetical equilibrium frequencies ($\chi^2 = 1.088; 0.30 > P > 0.20$). Likewise, there was no significant difference between the observed frequencies and the hypothetical equilibrium frequencies ($\chi^2 = 0.085$; $0.80 > P > 0.70$) of the *ca.* number 5 chromosomes (as in karyotype KC).

Next, chi-square analysis was performed after combining into one problem all of the karyotypic conditions, that is, in the manner of a Hardy-Weinberg problem involving two loci, each with two alleles. Thus there were nine possible karyotypes; analysis was performed using as one class each the three karyotypes observed in the population sample, with the six remaining rare karyotypes pooled into another class. This test also revealed no significant difference between the frequencies in the observed sample and those in the hypothetical equilibrium ($\chi^2 = 2.860$; $0.10 > P > 0.05$). Furthermore, a chi-square test for association with a 2 by 2 contingency table (after the necessary pooling following the original setting up of a 3 by 3 table that included all 9 hypothetical

karyotypes) revealed no association between the karyotypes ($\chi^2 = 1.486$; $0.30 > P > 0.20$).

These analyses reveal that the various karyotypes of *S. clarki* could be in equilibrium in southern Arizona. The rarest expected karyotype is that which is homozygous for both atypical conditions: $2n = 40$, composed of 20 (with a pair of the atypical subtelocentric *ca.* number 5) + 2 + 18. As its hypothetical frequency at equilibrium is 0.0000250, I am not astonished that it was not encountered in the sample!

This same problem was also approached from another direction. Considering the population sample at hand as P_1, I determined the expected frequency of each karyotype in the next generation (F_1). Only six of the nine hypothetical karyotypes could be obtained in this F_1 because not all hypothetical types of gametes in the population could be produced by the sample observed (e.g., there could not be produced in the first generation any individual homozygous for both atypical chromosomal conditions). All hypothetical karyotypes first appeared in calculating the expected F_2 generation; their frequencies did not reach equilibrium until the hypothetical F_{21} generation (carried out to seven decimal places). The expected frequency of each karyotype in this hypothetical F_{21} generation was remarkably close to that which was predicted by means of the much shorter method discussed immediately above, considering the amount of rounding necessary in carrying out these extensive calculations. Chi-square analysis comparing the hypothetical F_{21} with the observed sample (P_1), using as one class each the three karyotypes observed in the sample and the six remaining rare karyotypes pooled into another class, produced the same results obtained in the earlier analysis ($\chi^2 = 2.860$; $0.10 > P > 0.05$), again indicating that these karyotypes could be in equilibrium in southern Arizona.

The conclusions derived from these calculations must be considered tentative. They are based not only on the usual assumptions required with use of the Hardy-Weinberg formula, but also on the assumption that lizards from the Pajarito and Patagonia mountains can be treated as one population sample, and that no seasonal variation or other types of local variation affected the frequencies of the karyotypes during the collecting. The sample size itself, N = 51 lizards, is small for this type of analysis, and six theoretical karyotypes have not yet been observed. Future investigations will be directed toward obtaining additional critical data so as to more thoroughly explore these particular problems.

External Morphology: Examination of external morphology on the specimens comprising the sample from southern Arizona revealed no traits that were correlated with the atypical karyotypes. The following

TABLE 1

COMPARISON OF EXTERNAL MORPHOLOGICAL CHARACTERISTICS IN SPECIMENS OF *Sceloporus clarki* WITH TYPICAL AND WITH ATYPICAL KARYOTYPES

(No Significant Differences are Indicated.[a])

External Characteristics	Karyotypes		Student's *t*-test
	Typical	Atypical	
Femoral Pores	24.50±0.32	24.70±0.46	$t=0.36$
	(20–29)	(22–28)	$0.80>P>0.70$
	N=34	N=17	
Scales between Pore Series	8.88±0.16	8.94±0.22	$t=0.22$
	(7–11)	(8–11)	$0.90>P>0.80$
	N=34	N=17	
Dorsal Scales	31.50±0.26	31.70±0.46	$t=0.40$
	(29–35)	(28–35)	$0.70>P>0.60$
	N=34	N=17	
Scales around Midbody	38.06±0.23	38.12±0.46	$t=0.13$
	(35–40)	(35–42)	$0.90>P>0.80$
	N=31	N=16	
Body Length	89.03±3.14	79.76±4.97	$t=1.64$
	(43–114)	(49–110)	$0.20>P>0.10$
	N=34	N=17	

[a]Data presented are the mean ± the standard error of the mean, range (in parenthesis), and N = sample size. All lizards are from southern Arizona.

characteristics were analyzed: (1) total number of femoral pores, (2) number of scales medially separating the two series of femoral pores, (3) number of dorsal scales (occiput to rump), (4) number of scales around midbody, (5) body length (snout to vent), and (6) several characteristics of coloration and color pattern.

Several comparisons of the scale counts and length measurements were made with Student's *t*-tests. In one, all individuals possessing the typical karyotype were compared with those having atypical karyotypes, i.e., individuals with either atypical karyotype were pooled into one statistical sample. There was no significant difference between the samples for any of the characteristics examined (table 1).

For another set of *t*-tests, all individuals with the typical karyotype (KA) were compared with those having the 20+1+19 karyotype (KB). Again, there was no significant difference between the samples for any of the characteristics examined (table 2). Reliable comparisons could not be made between individuals possessing the typical karyotype and those possessing the atypical one having a subtelocentric number 5 chro-

TABLE 2

COMPARISON OF EXTERNAL MORPHOLOGICAL CHARACTERISTICS EXHIBITED IN SPECIMENS OF *Sceloporus clarki* WITH TYPICAL AND WITH ATYPICAL 20+1+19 KARYOTYPES (No Significant Differences are Indicated.[a])

External Characteristics	Karyotypes: Typical	Karyotypes: Atypical (20+1+19)	Student's *t*-test
Femoral Pores	24.50±0.32 (20-29) N = 34	25.00±0.54 (22-28) N=13	$t=0.81$ $0.50>P>0.40$
Scales between Pore Series	8.88±0.16 (7-11) N=34	8.92±0.24 (8-11) N=13	$t=0.013$ $P>0.90$
Dorsal Scales	31.50±0.26 (29-35) N=34	32.08±0.55 (28-35) N=13	$t=1.06$ $0.30>P>0.20$
Scales around Midbody	38.06±0.23 (35-40) N=31	38.08±0.56 (35-42) N=12	$t=0.04$ $P>0.90$
Body Length	89.03±3.14 (43-114) N=34	77.54±5.69 (49-110) N=13	$t=1.83$ $0.10>P>0.05$

[a] Data presented are the mean ± the standard error of the mean, range (in parenthesis), and N = sample size. All lizards are from southern Arizona.

mosome (KC) because of the small number of lizards (N=4) with the latter condition.

Of the characteristics tested, body length is the most likely to have been influenced by sexual dimorphism. Thus, body length was tested again, by comparing all of the females having the typical karyotype (N=11) with all of those having the 20+1+19 karyotype (N=9); again, there was no significant difference between the samples ($t=1.24$; $0.30>P>0.20$). This test was not repeated with the males because of the small sample size, but the test revealed no difference within a sex in comparing lizards with typical and those with atypical (20+1+19) karyotypes.

The analyses revealed no differences in external morphology between lizards with the typical karyotype and lizards with atypical ones. Surely, this is not to say that there are no differences whatsoever; quite possibly some differences, physiological if not morphological, exist. At any rate, there are no present indications as to the adaptive significance of the various karyotypes.

GEOGRAPHIC VARIATION AND ORIGIN: The frequencies of the different karyotypes in *S. clarki* vary geographically. Although the atypical karyotype heterozygous for a subtelocentric number 5 (KC) is known only from southern Arizona, the atypical 20+1+19 karyotype (KB) is known also from southern Sinaloa, Mexico (of two males collected at this last locality, one had the typical 20+0+20 karyotype and one had the 20 + 1 + 19). All the remaining 28 specimens of *S. clarki* examined had the typical karyotype (KA). This includes 16 individuals from the Navojoa-Alamos area of southern Sonora, Mexico, and 12 lizards from seven other localities in Arizona, New Mexico, and Sinaloa. Thus, the atypical karyotypes are now known from near both the northern and southern extremes in the range, but not in a sizable population sample (N=16) from in between (southern Sonora); and perhaps they occur in low frequencies elsewhere.

Although it is most likely that each of the two different aberrations resulting in the two atypical karyotypes arose independently, it is unlikely that the same 20+1+19 karyotype (KB) evolved twice independently (once in the north and once in the south). Indeed, as this 20+1+19 karyotype occurs near the extremes of the range of *S. clarki,* and as a similar, if not identical, one occurs in *Sceloporus melanorhinus* (a more tropical species presumably ancestral to *S. clarki;* see below), perhaps it occurred as a karyotypic variant in the ancestral population from which *S. clarki* was derived. This hypothesis is supported by the evidence (above) that the atypical and typical karyotypes may occur in an equilibrium, at least in particular places under particular circumstances. The atypical karyotype KC (heteromorphic *ca.* number 5) that occurs in *S. clarki* probably resulted from a more recent aberration (subsequent to derivation of the species), since the same condition is not known in *S. melanorhinus* (although a similar one is).

The specimens examined represent the subspecies *S. clarki clarki* and *S. c. boulengeri.*

Sceloporus melanorhinus

Detailed analysis of 143 mitotic bone marrow cells from seven individuals (three males, four females) revealed the occurrence of three karyotypes in *Sceloporus melanorhinus.* The three males had one karyotype while the other two karyotypes were equally distributed among the four females. These karyotypes are similar to those of *Sceloporus clarki,* as follows:

KARYOTYPE KA: This karyotype is extremely similar, if not identical, to the typical one (KA) of *S. clarki* (20+0+20; compare figs. 1A and 4A). The secondary constriction also occurs on the tip of the long arm

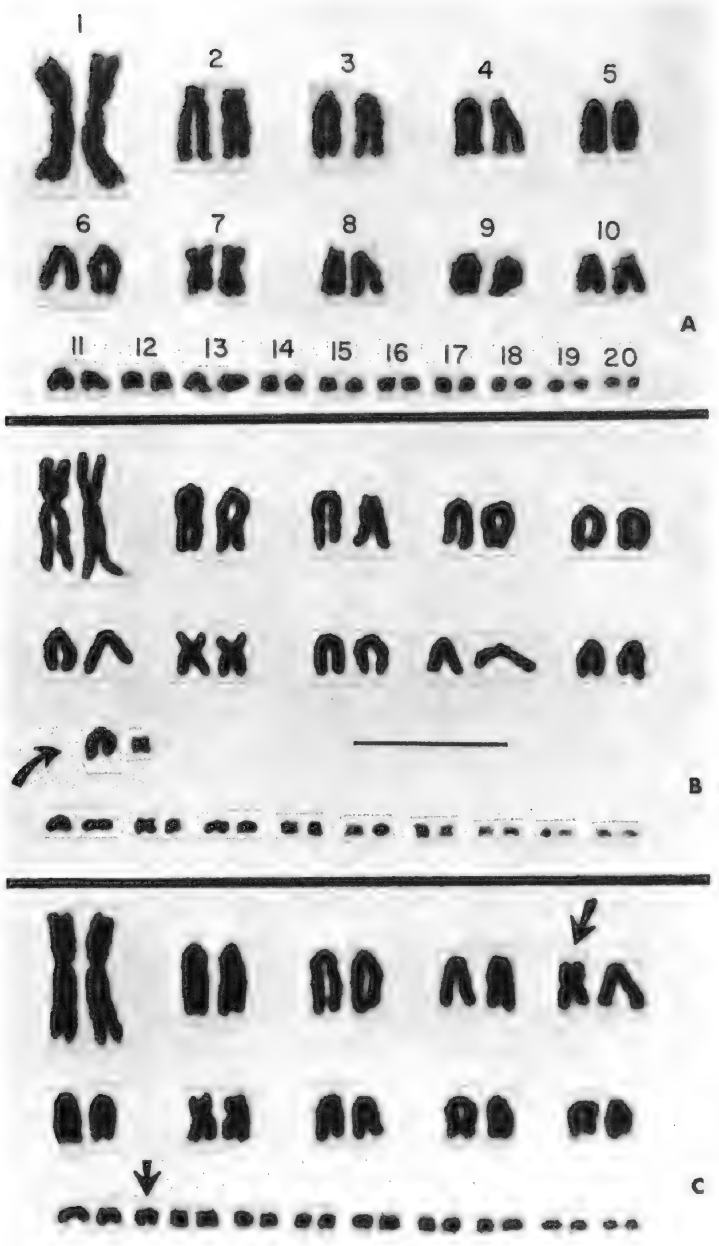

FIG. 4. Chromosomes of three specimens of *Sceloporus melanorhinus*. A. Karyotype KA ($2n = 40$), described on pages 14–16; U.A.Z. No. 28300, female. B. Karyotype KB ($2n = 40$), described on page 16; arrow indicates heteromorphic pair; line represents 10 μ; U.A.Z. No. 28302, female. C. Karyotype KC ($2n = 39$), described on page 16; arrows indicate heteromorphic pair (upper) and "unpaired" microchromosome (lower); U.A.Z. No. 28299, male.

of chromosome number 1. This karyotype occurred in a female from Tuxtla Gutiérrez, Chiapas, Mexico, and also in a female from near Colima, Colima, Mexico (only six cells were analyzable on the slides from the last individual; in each of these the macrochromosomes were clearly of this constitution, but the precise number of microchromosomes, about 20, could not be determined).

KARYOTYPE KB: This karyotype is extremely similar, if not identical, to the atypical 20+1+19 one of *S. clarki* (compare figs. 1B and 4B). It occurred in two females from Acapulco, Guerrero, Mexico.

KARYOTYPE KC: This karyotype is similar to the atypical one of *S. clarki* in which there is an atypical subtelocentric macrochromosome that pairs with a telocentric (compare figs. 1C and 4C). In *S. melanorhinus* it also appears to involve pair *ca.* number 5; however, the "odd" bi-armed macrochromosome is metacentric, rather than subtelocentric as in *S. clarki*. Another difference is that this atypical karyotype has only 19 microchromosomes instead of 20 and thus one appears unpaired. Three males (two from near Colima, Colima, Mexico, and one from Acapulco, Guerrero, Mexico) had this karyotype.

Presumably karyotypes KA and KB behave regularly in meiosis as they do in *S. clarki;* this may be so for karyotype KC also, but the fate of the "lost" microchromosome in this karyotype remains, for the present, unknown. Since the lizards were not collected during the breeding season and the peculiarities of their karyotypes were not known until after the animals were killed, additional field work is necessary to obtain meiotic material for analysis. More samples will also be necessary to determine local frequencies and distributions of the various karyotypes, and to determine whether any of them are sex correlated. Although individuals of both sexes of *S. clarki* can possess a karyotype generally similar to type KC of *S. melanorhinus,* it is suggestive that the three males of *S. melanorhinus* all had that one karyotype, whereas none of the four females did.

Karyotypes KA and KB are presumably both very old and surely older than KC. Form KA evidently occurs throughout the range of the species, since it has been found in animals from Tuxtla Gutiérrez and from Colima. Form KB apparently was derived from KA and existed as a variant in the *S. melanorhinus* or *melanorhinus*-like populations from which *Sceloporus clarki* was derived (see above). Karyotype KC presumably arose following more recent chromosomal aberrations.

The specimens examined represent the subspecies *S. melanorhinus calligaster* and *S. m. stuarti.*

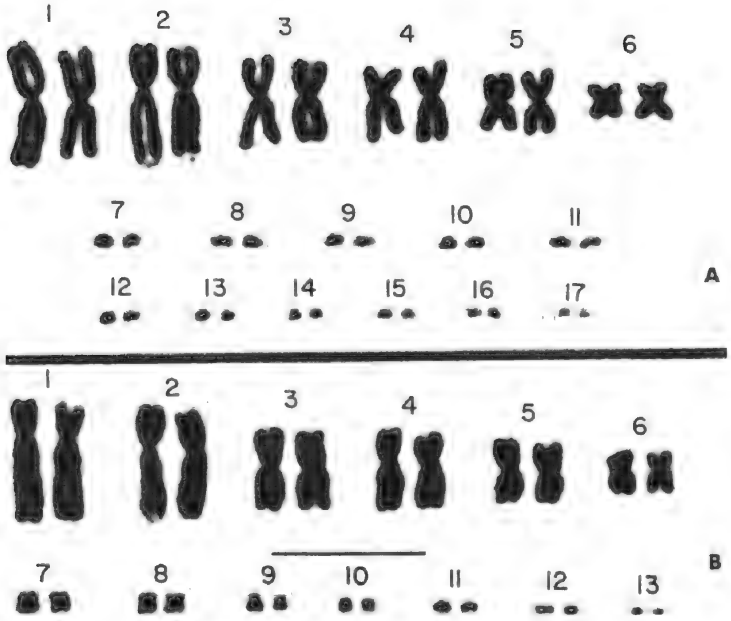

FIG. 5. Karyotypes of *Sceloporus orcutti* and *Sceloporus magister*. A. *Sceloporus orcutti* ($2n = 34$), U.A.Z. No. 21674, female from near Banning, San Jacinto Mountains, Riverside County, California. B. *Sceloporus magister* ($2n = 26$), U.A.Z. No. 24197, male from near Desemboque del Río San Ignacio, Sonora, Mexico. Line Represents 10 μ.

Sceloporus orcutti

Detailed analysis of more than 73 mitotic bone marrow cells from eight individuals (four of each sex) revealed that $2n = 34$ chromosomes in *S. orcutti*, a considerably lower number than occurs in its southern relatives considered above. The karyotype (fig. 5A) consists of 12 large, conspicuously bi-armed macrochromosomes (six pairs) plus 22 microchromosomes (11 pairs). Of the macrochromosomes, numbers 1 and 5 are metacentric, while numbers 2 (most conspicuously), 3 (very less so), 4, and 6 (very less so) are submetacentric; there is a satellite on the tip of the long arm of number 2. The microchromosomes are mostly telocentric, one larger pair rarely appearing subtelocentric. Excepting numbers 3 and 4, which often appear similar, the macrochromosome pairs are individually recognizable with high confidence in most cells, while the microchromosomes are not.

The specimens examined represent both subspecies, *S. orcutti orcutti*, and *S. o. licki*.

Sceloporus magister

The diploid number of 26 chromosomes has been verified by examination of approximately 142 cells from 16 lizards (nine males, seven females). The karyotype (fig. 5B), as earlier described by Lowe, Cole and Patton (1967), is comprised of six pairs of macrochromosomes and seven pairs of smaller elements; the latter include four pairs of smaller microchromosomes similar in size to those in *S. clarki,* and three pairs of larger metacentrics that are approximately twice as large.

The macrochromosomes are similar to those of *S. orcutti* except that number 1 is most conspicuously submetacentric and number 3 is metacentric. Of the smaller pairs, 7, 8, and 9 are metacentric, 10 is subtelocentric, and the rest (11 through 13) are telocentric. In most cells all the macrochromosomes are clearly recognized individually; the smaller chromosomes, particularly 7 and 8, and 11 and 12, cannot be labeled with certainty.

Specimens examined represent the subspecies *S. magister magister, S. m. cephaloflavus,* and *S. m. uniformis.*

Sceloporus lundelli

The karyotypes of *S. lundelli* were determined and verified by examining 166 cells from 13 lizards (eight males, five females). These karyotypes have only 22 chromosomes, which is also the normal diploid number possessed by the remaining species in the *spinosus* group and is the lowest known chromosome number in the genus *Sceloporus* (see Lowe, Wright, and Cole, 1966). Unlike most species of the *spinosus* group, however, *S. lundelli* has conspicuous sex correlated chromosomes of the X-Y type (fig. 6).

The karyotypes (fig. 6) are composed of six pairs of macrochromosomes and five pairs of smaller elements. Of the former, numbers 1, 3, 4, and 5 are metacentric, while numbers 2 (most conspicuously) and 6 (much less so) are submetacentric. Pair number 2 bears a terminal satellite as in the two species considered immediately above. In females, both chromosomes of the largest pair in the smaller group (number 7) are telocentric (X-X). Males, however, exhibit one individual number 7 that is telocentric and one that is subtelocentric (X-Y). The remaining chromosomes appear to be two pairs that are metacentric or nearly so (numbers 8 and 9), one pair that is subtelocentric (number 10), and one pair that is telocentric (number 11). The chromosomes are readily recognized individually in most cells, excepting numbers 3 and 4, and numbers 8 and 9, which are very similar to one another.

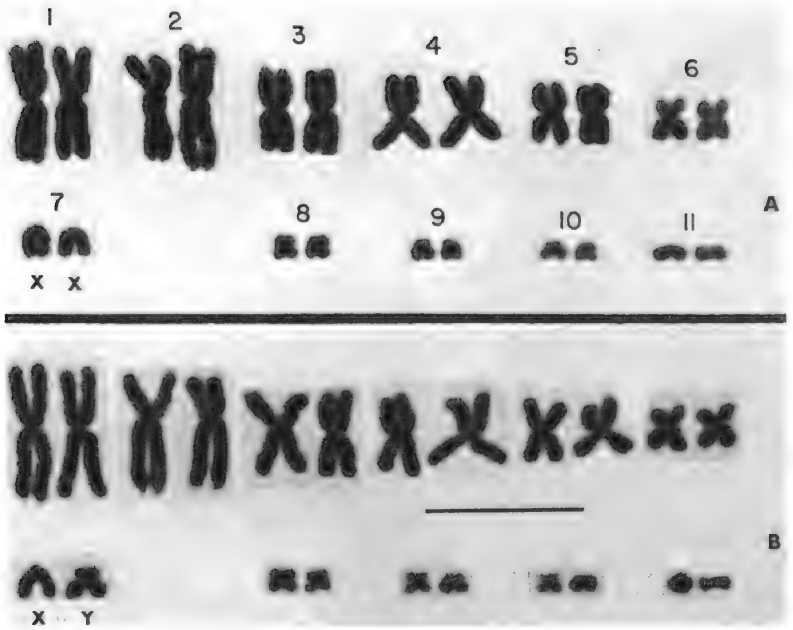

FIG. 6. Karyotypes of *Sceloporus lundelli* ($2n = 22$). A. Female, with two X chromosomes (no. 7); U.A.Z. No. 28345, from Pisté, Yucatan, Mexico. B. Male, with one X and one Y chromosome (no. 7); U.A.Z. No. 28340, from near Río Lagartos, Yucatan, Mexico. Line represents 10 μ.

The karyotypic sexual dimorphism in pair number 7 is consistent: all eight males had the heteromorphic pair; all five females had the homomorphic pair of telocentric chromosomes. Thus this is referred to as an X-Y sex chromosome system.

Examination of testicular material demonstrated that there are six machrochromosome bivalents and five smaller bivalents in primary spermatocytes (fig. 7A), and that segregation is regular and apparently undisturbed in the heteromorphic sex. Analysis of 50 secondary spermatocytes at metaphase II (fig. 7B, C) revealed 30 containing the X and 20 containing the Y chromosome; as these frequencies are not significantly different from the hypothetical 1:1 ratio ($\chi^2 = 2.000$; $0.20 > P > 0.10$), I conclude that X-bearing and Y-bearing spermatozoa are produced in equal frequency.

Most species of *Sceloporus* do not exhibit readily recognizable sex chromosomes. Members of the *torquatus* species group, however, are exceptional in this regard (Cole, Lowe, and Wright, 1967). Those species have an $X_1X_2Y(\delta):X_1X_1X_2X_2(\varphi)$ system rather than this simpler one of

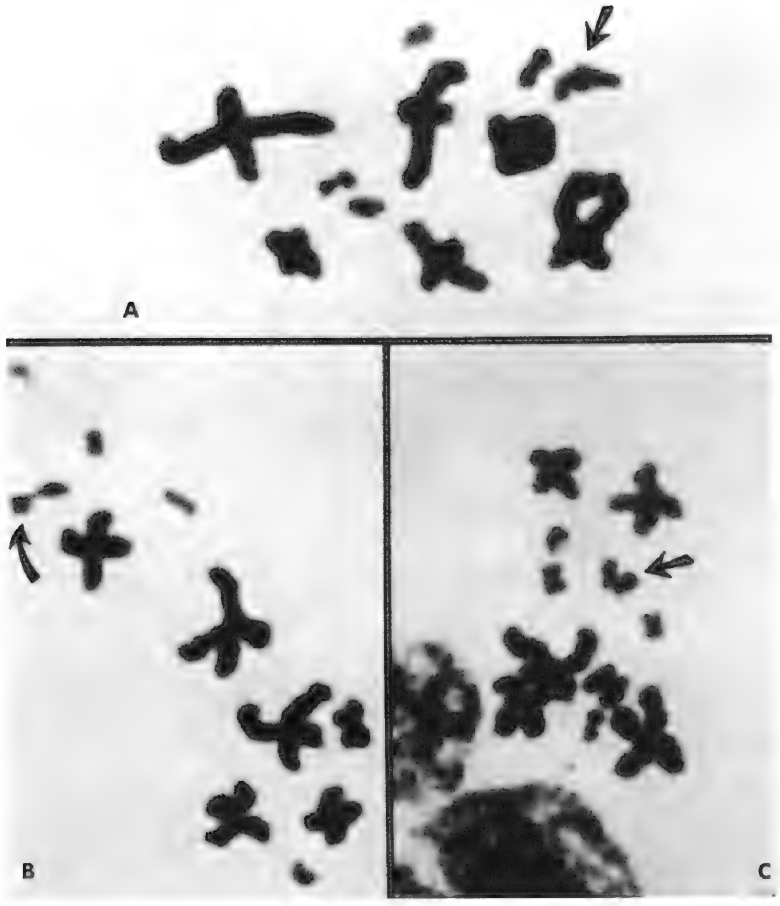

FIG. 7. Spermatocytes of *Sceloporus lundelli*. A. Primary spermatocyte (metaphase I), with six bivalents of macrochromosomes + five bivalents of smaller ones ($n = 11$). Arrow indicates heteromorphic X-Y pair (no. 7); U.A.Z. No. 28339, male from near Río Lagartos, Yucatan, Mexico. B. Secondary spermatocyte (metaphase II), with 6 + 5 constitution ($n = 11$), containing telocentric X chromosome [no. 7 (arrow)]; U.A.Z. No. 28337, male from Pisté, Yucatan, Mexico. C. Secondary spermatocyte (metaphase II), with 6 + 5 constitution ($n = 11$), containing subtelocentric Y chromosome [no. 7 (arrow)]; U.A.Z. No. 28340, male (fig. 6B).

XY(♂):XX(♀), and their Y chromosome is metacentric rather than subtelocentric. It is particularly noteworthy nonetheless, that the Y chromosomes of both systems are approximately the same size and presumably they both evolved in part, at least, by means of centric fusion of

microchromosomes (see below). Thus these particular chromosomes may contain some historically identical gene loci that are directly concerned with sex determination. If this is so, these sex-determining loci presumably are still located on particular microchromosomes of such species as *Sceloporus clarki* and *S. orcutti,* in which the microchromosomes have not undergone centric fusion, hence indicating a major role for at least some of these dotlike chromosomes that certain investigators may consider insignificant merely because of their minute size. Indeed, Pennock, Tinkle, and Shaw (1969) have recently reported sex chromosomes among the microchromosomes of sceloporine lizards in the genus *Uta.*

The 13 specimens examined represent the subspecies *S. lundelli gaigeae.*

Sceloporus edwardtaylori

The 83 cells analyzed from nine individuals (six males, three females) exhibited $2n = 22$ chromosomes generally similar to those of *S. lundelli,* but with heteromorphic sex chromosomes conspicuously absent (fig. 8A). The six pairs of macrochromosomes are nearly identical to those of *S. lundelli,* the most conspicuous difference being the lack of the satellites on number 2. Of the five pairs of smaller chromosomes, numbers 7, 8, 10, and 11 are metacentric or submetacentric, while number 9 is subtelocentric. An inconspicuous satellite occurs terminally on one arm of pair number 8.

As this is the only species in the group having the satellite on number 8, and as all other species in the group, including more primitive and more derived forms (see below), have the satellite occurring terminally on number 2, it is likely that the altered position in *S. edwardtaylori* resulted from a translocation of the satellite chromatin from number 2, assuming that the chromatin in the secondary constriction and satellite represents the same loci in these species. The translocated segment must be small since chromosome numbers 2 and 8 do not appear different in size from those in their related species and the centromere position in number 2, in particular, appears the same. Thus, disregarding the satellite, chromosome number 2 of *S. edwardtaylori* is morphologically similar to that of *S. lundelli.*

Sceloporus olivaceus

Sceloporus olivaceus also has $2n = 22$ chromosomes, which was determined and verified by analysis of more than 200 dividing cells from 12 individuals (five males, seven females). Normally the karyotype (fig. 8B) is nearly identical to that of *S. edwardtaylori* (fig. 8A). Their six pairs of

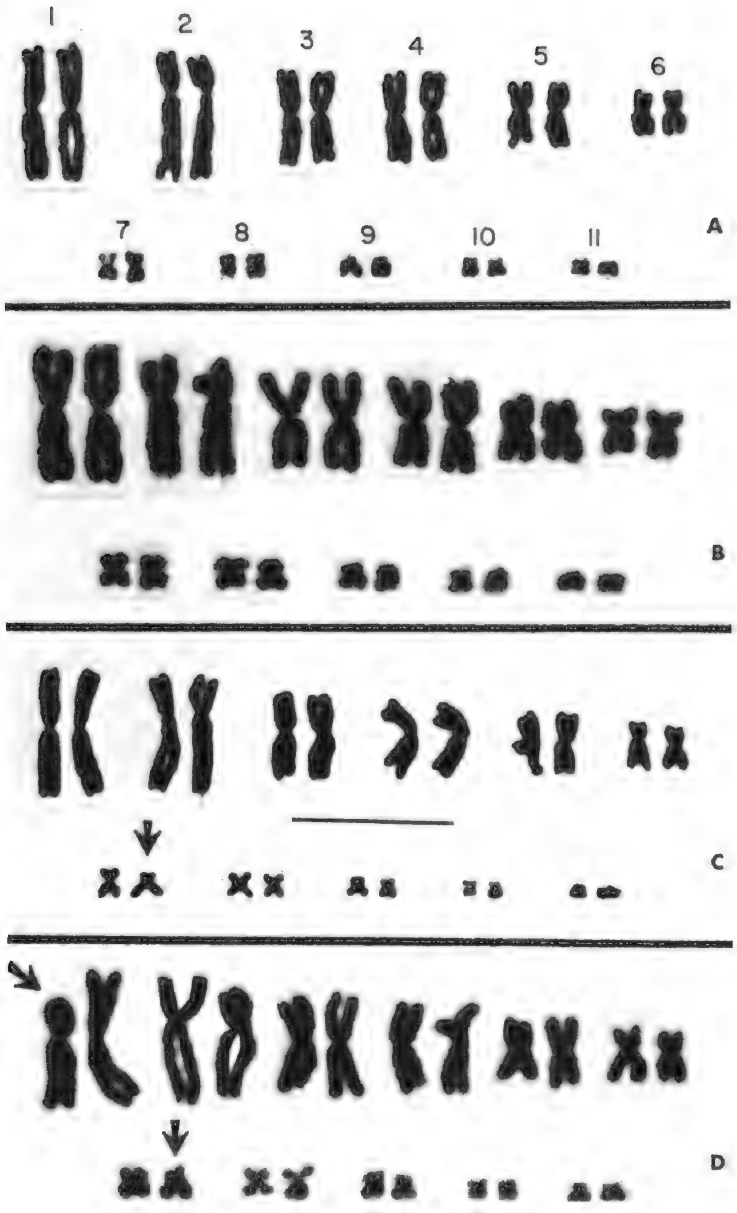

FIG. 8. Karyotypes of two species of *Sceloporus*. A. *Sceloporus edwardtaylori* ($2n = 22$), U.A.Z. No. 28371, female. B. *Sceloporus olivaceus* ($2n = 22$); both elements of pair number 7 are typically metacentric; U.A.Z. No. 28328, male. C. *Sceloporus olivaceus;* atypical, with pair number 7 heteromorphic [one chromosome is metacentric and one is subtelocentric (arrow)]; line represents 10 μ; U.A.Z. No. 24205, male. D. *Sceloporus olivaceus;* aberrant cell from same lizard (C); pair number 7 is heteromorphic (lower arrow) and pair number 1 includes a chromosome with a loop (upper arrow; see description on pages 24–25).

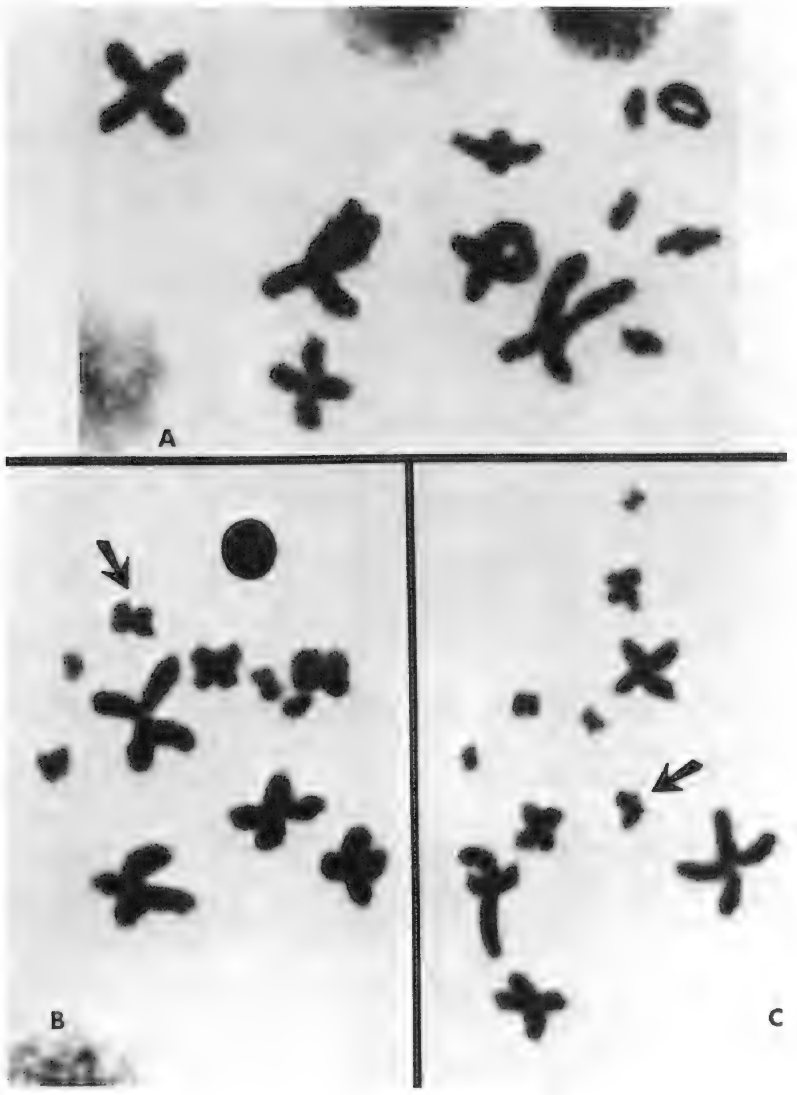

FIG. 9. Spermatocytes from individual of *Sceloporus olivaceus* with atypical heteromorphic pair of chromosomes (no. 7); all three cells are from U.A.Z. No. 24205, male (fig. 8C, D). A. Primary spermatocyte (metaphase I), with six bivalents of macrochromosomes + five smaller bivalents ($n = 11$). B. Secondary spermatocyte (metaphase II), with six macrochromosomes and five smaller chromosomes ($n = 11$). Number 7 (arrow) is typical metacentric element. C. Secondary spermatocyte (metaphase II), with six macrochromosomes and five smaller chromosomes ($n = 11$). Number 7 (arrow) is atypical subtelocentric element.

macrochromosomes conspicuously differ only in the presence in *S. olivaceus* of the secondary constriction terminally on chromosome number 2. In other words, the macrochromosomes of *S. olivaceus* are exceedingly similar, if not identical, to those of *S. lundelli.* The five pairs of smaller chromosomes include four (numbers 7–10) that are metacentric or nearly so, and the fifth pair (number 11), which is subtelocentric or submetacentric.

Two individuals were characterized by an atypical karyotype. In these (fig. 8C), number 7 is a heteromorphic pair having one metacentric element (typical) and one subtelocentric (atypical). Thus these individuals appear to be heterozygous for a pericentric inversion in pair number 7. This is not a sex-correlated phenomenon since it occurred in one specimen of each sex. In the male, testicular tissues exhibited the same heteromorphism as bone marrow tissues.

The aberration involved with this heteromorphic pair is not of very different magnitude from those in the heterozygotes in *Sceloporus clarki* (see above). Furthermore, the specimens possessing it were from different localities; the male was from northwest of Del Rio, along the Devil's River, Val Verde County, Texas, and the female was from Austin, Travis County, Texas. Thus it is not surprising that meiosis proceeded regularly in the heterozygous male, as it does also in the *Sceloporus clarki* heterozygotes (see above). Six bivalents of macrochromosomes and five of smaller chromosomes are regularly formed in meiosis I (fig. 9A). Segregation is normal and produces both types of expected secondary spermatocytes (those with the atypical subtelocentric number 7 and those with the typical metacentric one; fig. 9B, C) with equal frequency, as determined by analysis of 50 cells at metaphase II ($N = 21$ typical; $N = 29$ atypical; $\chi^2 = 1.28$; $0.30 > P > 0.20$). This suggests that individuals that are homozygous for the atypical subtelocentric number 7 occasionally may be produced, although they have not yet been observed.

One other aberration was found in one bone marrow cell of the same aberrant male. This cell contained 12 macrochromosomes and 10 smaller chromosomes as is typical, except that one macrochromosome had an unusually short arm that exhibited sister chromatid fusion, thus forming a loop (fig. 8D). This is nearly identical to the chromosomal aberration in *Sceloporus virgatus* recently reported by Cole and Lowe (1968). Indeed, even the same chromosome (one of the number 1 homologues) is involved. Similarly, this presumably resulted from a break in the arm and was followed by sister chromatid fusion. But no acentric fragment occurred in this particular cell (fig. 8D), suggesting that the aberration occurred in one of its ancestral cells and the fragment had since been

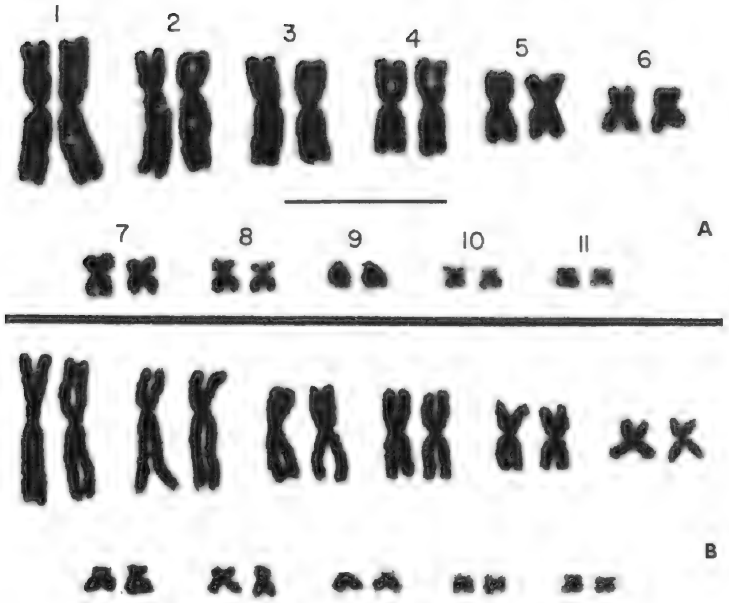

FIG. 10. Karyotypes of *Sceloporus spinosus* ($2n = 22$). A. Individual with pair number 7 metacentric; U.A.Z. No. 28355, female from 5 miles (by Mex. 175) northwest of Miahuatlán, Oaxaca, Mexico. Line represents 10 μ. B. Individual with pair number 7 subtelocentric; U.A.Z. No. 28354, female from near Celaya, Guanajuato, Mexico.

lost (or passed into the other daughter cell). Thus it appears that at least certain types of bone marrow cells of *S. olivaceus* can survive the deletion of a sizable portion of a number 1 chromosome, even while already supporting an atypical heteromorphic pair (number 7).

Sceloporus spinosus

Examination of more than 65 mitotic bone marrow cells from five animals (one male, four females) revealed two very similar but distinct karyotypes that appear to be geographically rather than sexually correlated, and neither of which has heteromorphic pairs of chromosomes. One of these karyotypes occurs in the animals from the vicinity of Miahuatlán and Oaxaca de Juárez, Oaxaca, Mexico (fig. 10A; N = 3 females), and the other occurs in the specimens from south of Celaya, Guanajuato, on the Mexican Plateau (fig. 10B; N = 2 specimens, one of each sex).

In both karyotypes the diploid number of 22 includes six pairs of macrochromosomes that are essentially indistinguishable from those of

S. lundelli, S. edwardtaylori, and *S. olivaceus* (the satellite is on number 2 as in *S. lundelli* and *S. olivaceus*) plus five pairs of smaller elements (fig. 10A, B). The Miahuatlán and Oaxaca de Juárez animals (*S. spinosus apicalis* and *S. spinosus caeruleopunctatus,* respectively) have among the five pairs of smaller chromosomes four that are metacentric to submetacentric (numbers 7, 8, 10, and 11) and one that is subtelocentric (number 9). In the specimens of *S. spinosus* from near Celaya (*S. spinosus spinosus*), pairs 8 through 11 are as just described, but number 7 is subtelocentric rather than metacentric (fig. 10A, B). The difference between these karyotypes probably results from a pericentric inversion.

Specimens examined include representatives of the subspecies *S. spinosus spinosus, S. s. apicalis,* and *S. s. caeruleopunctatus.* Future collecting will be designed to determine whether the geographic distribution of the karyotypic forms corresponds well with that of the subspecies, and the consequences when they approach one another or meet.

Sceloporus horridus

This species also has a diploid number of 22 composed of six pairs of macrochromosomes and five pairs of smaller ones, which was determined and verified by examination of nearly 100 mitotic bone marrow cells from eight individuals (six males, two females). As in *S. spinosus,* there are two distinct though similar karyotypes (fig. 11) that appear to be geographically correlated, and which do not involve heteromorphic pairs of chromosomes within individuals. One of the karyotypes occurs in the lizards from two localities in Nayarit, Mexico, and the other occurs in the specimens from four other widely separated Mexican localities: (1) near Colima, Colima, (2) Autlán, Jalisco, (3) the vicinity of Iguala, Guerrero, and (4) 7 miles (by road) northwest of Teotitlán del Camino (Oaxaca), Puebla, Mexico.

In both cases the six pairs of macrochromosomes are extremely similar to, if not identical to, those of *S. spinosus,* including even the terminal location of the satellites on chromosome number 2. The Nayarit specimens (*S. horridus albiventris*) have all of the five smaller pairs (7 through 11) metacentric or nearly so (fig. 11A). Karyotypes in the animals (*S. h. horridus* and *S. h. oligoporus*) from the other localities are exceedingly similar, but chromosome number 7 is clearly telocentric or essentially so, rather than metacentric (fig. 11B). As in *S. spinosus,* it is most likely that this karyotypic difference results from a pericentric inversion.

Specimens examined include representatives of the three subspecies, *S. horridus horridus, S. h. albiventris,* and *S. h. oligoporus.* Future field and laboratory work is expected to elucidate more clearly the geographic and

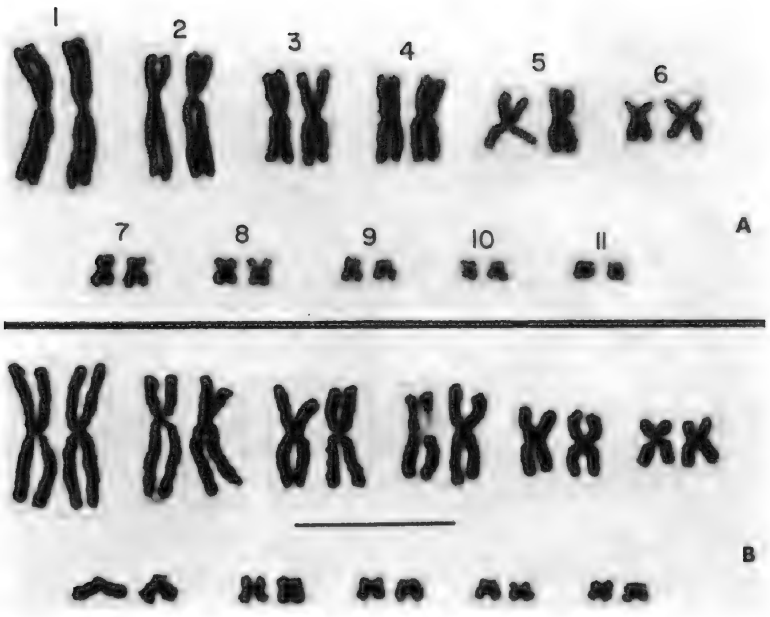

FIG. 11. Karyotypes of *Sceloporus horridus* ($2n = 22$). A. Individual with pair number 7 metacentric; U.A.Z. No. 28315, male from 8 miles (by Mex. 15) southeast of Tepic, Nayarit, Mexico. B. Individual with pair number 7 telocentric or essentially so; U.A.Z. No. 28324, male from near Colima, Colima, Mexico. Line represents 10 μ.

taxonomic relationships of these karyotypic forms. For the present, it appears that one chromosome form (metacentric number 7) is restricted to *S. h. albiventris,* while the other form occurs in the other subspecies.

EVOLUTION

Opening Remarks

I take up consideration of phylogenetic relationships within this group of lizards, fully aware that conclusions regarding phylogenies based only on traits of Recent species (the fossil record of *Sceloporus* is practically nonexistent) can be rather tenuous. Although many biologists feel that such phylogenetic speculations are futile, the great value of karyotypic data in providing a basis for hypothesizing on evolutionary relationships is clear in many instances (for reviews see Stebbins, 1950; Patterson and Stone, 1952; White, 1954). For example, karyotypic analysis has revealed with virtual certainty the ancestry of particular species of lizards (Lowe and Wright, 1966).

I shall present the evolutionary relationships within the *spinosus* group as I see them, without a greatly detailed discussion of the numerous possible schemes that might be preferred by others. To provide "equal time" to all such alternatives would seriously cloud the story to be outlined below. I recognize that minor points may well be quibbled over interminably, and some investigators may even wish to twist the picture 180 degrees. To the latter I bid good luck, for to convince me of a considerably different phylogeny within this group would necessitate educating me further in areas of which I am now ignorant, hopefully not to the point of hopelessness.

Characteristics

External Morphology: Attempts at determining phylogenetic relationships among *spinosus* group species on the basis of classical characteristics of scutellation and color pattern are considerably frustrating. I have reviewed these characteristics in detail as presented by Smith (1939) for the various species, and I have re-examined most of them on series of specimens of each species. While these traits of external morphology serve to distinguish between the species, most of them do not exhibit evolutionary trends or tendencies of conspicuous utility for phylogenetics. Indeed, in many cases the species must even be diagnosed on the basis of combinations of several detailed characteristics.

A number of characteristics (e.g., number of canthal scales, number of loreals, and number of postrostrals) exhibit considerable similarities in expression from species to species and are therefore useless for inferring relationships within the *spinosus* group. Certain other traits are of little phylogenetic value because they characterize only one species, to which they may be particularly adaptive. For example, the gross morphology of the scales at particular places on the body does not vary vastly from species to species in this group, one obvious exception being the reduced spines and keels on the dorsal body scales of *Sceloporus orcutti;* presumably this is an adaptive response to its petricolous mode of life, which is more highly developed than in any other species of the group. There are also traits with no apparent adaptive significance that characterize only one species (e.g., the outer row of labiomentals regularly contacts the mental in *S. magister* but not in any of the other species); these likewise are of no direct use in reconstructing the phylogeny of this group.

Other specific characteristics more frequently used in saurian classification suffer from similar or additional deficiencies when examined with a view toward evolutionary relationships within the *spinosus* group. Variation in the mean number of dorsal scales, for example, ranges only from

about 29 (e.g., in *S. melanorhinus*) to about 36 (e.g., in *S. orcutti licki*); and most of the species appear to exhibit little intraspecific variation in this characteristic. Nevertheless, among the subspecies of *Sceloporus magister* there are significant differences in dorsal scale counts, with population means from different localities varying from about 29 to about 34 (Smith, 1939; Phelan and Brattstrom, 1955), which encompasses almost the entire range of variation for the species group and suggests that the trait may be relatively easily molded locally by selection and/or drift. Analysis of the number of scales around midbody, number of ventral scales, and number of femoral pores produces similar results.

The dilemmas just considered are not surprising. After all, these species are considered as comprising a group of closely related forms precisely because of their similarities in external morphology and the scarcity of sharply demarcated differences between them. Thus, phylogenetic relationships within the group presently can best be inferred primarily from cytogenetic, biogeographic, ecological, and behavioral characteristics.

KARYOTYPES: There are four general karyotypes in the nine species of the *spinosus* group (table 3), disregarding for the moment the intraspecific variation and minor interspecific differences described in detail above. These four can be summarized briefly as follows: (1) the *melanorhinus*-type, in which $2n = 40$, composed of 20 macrochromosomes (10 pairs, of which two are submetacentric and eight are telocentric) plus 20 microchromosomes (10 pairs); (2) the *orcutti*-type, in which $2n = 34$, composed of 12 macrochromosomes (six pairs, of which two are metacentric and four are submetacentric) plus 22 microchromosomes (11 pairs); (3) the *magister*-type, in which $2n = 26$, composed of 12 macrochromosomes (six pairs, of which two are metacentric and four are submetacentric) plus 14 smaller chromosomes (seven pairs, of which only four are really small enough to qualify as microchromosomes); and (4) the *lundelli*-type, in which $2n = 22$, composed of 12 macrochromosomes (six pairs, of which four are metacentric and two are submetacentric) plus 10 smaller chromosomes (five pairs, none of which is small enough to qualify as microchromosomes).

The nine *spinosus* group species are arranged in four sets of related forms on the basis of karyotypic similarities (table 3). I do not doubt that this grouping reflects phylogenetic affinities, as it is based on cytogenetic characteristics of closely related populations. From the standpoint of karyotypic evolution by means of chromosomal centric fusions (whole-arm translocations; Robertson, 1916; see White, 1954, for a review), which has been shown to be compatible with hypotheses of amphibian and reptilian evolution both in a broad sense (e.g., Matthey, 1951) and

at the specific level in some cases (e.g., Lowe, Cole, and Patton, 1967), three most likely phylogenies are suggested by the karyotypes occurring in the *spinosus* group (table 3): (1) one general evolutionary line of centric fusions from the *melanorhinus*-type ($2n = 40$, with numerous telocentrics) through the *orcutti*- and *magister*-types, and terminating most recently in the *lundelli*-type ($2n = 22$, with nearly all, if not all, meta-

TABLE 3

OCCURRENCE OF THE FOUR GENERAL KARYOTYPES IN THE NINE *spinosus* GROUP SPECIES OF *Sceloporus*

melanorhinus-type ($2n=40$)	*orcutti*-type ($2n=34$)	*magister*-type ($2n=26$)	*lundelli*-type ($2n=22$)
S. melanorhinus	*S. orcutti*	*S. magister*	*S. lundelli*
S. clarki			*S. edwardtaylori*
			S. olivaceus
			S. spinosus
			S. horridus

centrics and submetacentrics); (2) two phylads, one of which involved a progression of centric fusions represented today by the sequence from the *melanorhinus*-type through the *orcutti*-type to the *magister*-type, and the other of which also involved centric fusion, and of which only the most advanced karyotypic forms (the *lundelli*-type) remain today; and (3) three phylads, one of which involved little karyotypic evolution and which is represented today by the *melanorhinus*-type (referred to hereafter as the *melanorhinus* subgroup), one of which involved several centric fusions and which is represented today by the *orcutti*- and *magister*-types (referred to hereafter as the *orcutti* subgroup), and the other of which also involved several centric fusions and which is represented today by the *lundelli*-type (referred to hereafter as the *lundelli* subgroup); but hypothesizing that the two lines involving fusions had a common ancestor in which the macrochromosomes had undergone fusion, precludes the presumption that all of these fusions occurred twice independently (fig. 16). The last hypothesis mentioned (3) is most compatible with the ecological and biogeographic relations of these species (see below).

The proposal that centric fusion of macrochromosomes was involved in the karyotype evolution of *spinosus* group lizards (Lowe, Cole, and Patton, 1967) was recently challenged by Gorman, Baptista, and Bury (1969). They concluded that the one primitive karyotype ancestral to all sceloporine iguanids had a diploid number of 34, composed of 12 bi-armed

macrochromosomes plus 22 microchromosomes (referred to in abbreviated fashion as a 12+22 karyotype), which is similar to the karyotype of *Sceloporus orcutti.* Their report followed that of Gorman, Atkins, and Holzinger (1967), in which it was concluded that the one primitive karyotype ancestral to the lizard family Iguanidae had a diploid number of 36, composed of 12 bi-armed macrochromosomes plus 24 microchromosomes (= a 12+24 karyotype). These conclusions are based on the assumption that the general karyotypic condition found in the majority of the species that were available for sampling, at whatever level of the taxonomic heirarchy one happened to be working with, was, therefore, the most primitive. While it is possible that these authors reached the correct conclusions, I am not yet convinced that their argument is sufficient. If I were to accept their proposed 12+22 karyotype as ancestral to the *spinosus* group of *Sceloporus,* then I would view *S. orcutti* of semiarid habitats in southern California and Baja California as ancestral to this group, which extends from tropical forests in northern Central America to arid deserts in the southwestern United States. The problem is even more complex, however, for if I were to simply employ the principal on which these authors' arguments are based, I would reach a rather different conclusion for the *spinosus* group; in this group, the general karyotype of the *lundelli* subgroup (12 bi-armed macrochromosomes plus 10 smaller chromosomes, most of which are clearly bi-armed; a 12+10 karyotype) would then be considered ancestral because it occurs in five of the nine species in the species group and none of the other three remaining general karyotypes of the group is represented in more than two species.

Ecology and Biogeography: The ecological preferences of the *spinosus* group species, together with their geographic distributions, may also be suggestive in regard to their phylogenetic relationships. The northernmost species (*S. magister*) is primarily a desert and desert-grassland form; the remaining species occur in similar habitats or generally in more southern subtropical to tropical habitats (e.g., thorn scrub; short-tree forest), which support plant communities ancestral to those of the relatively recently derived deserts, which evolved during the Tertiary Period largely in response to gradually increasing aridity (Chaney, 1940, 1947; Axelrod, 1948, 1950a, 1950b, 1958, 1960; Dorf, 1960). Independent investigations with a variety of groups of amphibians and reptiles have demonstrated considerable compatibility with the cited paleobotanical investigations, with occasional illustrative examples having been selected from desert- and desert-edge-dwelling pairs of *spinosus* group species of *Sceloporus* (Lowe, 1950, 1959; Norris, 1958; Savage, 1960, 1966; Auffenberg, 1963; Brame and Wake, 1963; Tihen, 1964; Wake, 1966; Asplund,

TABLE 4

GENERAL HABITAT AND BEHAVIORAL PREFERENCES OF THE NINE *spinosus* GROUP SPECIES OF *Sceloporus*

Species	Habitat	Behavior
	(A) *melanorhinus* subgroup	
S. melanorhinus	Semi-humid; tropical deciduous forest	Highly arboreal
S. clarki	Semiarid; tropical deciduous forest, subtropical thorn forest, oak-pine woodland	Arboreal
	(B) *orcutti* subgroup	
S. orcutti	Semiarid to arid; rocks in subtropical thorn forest, oak-pine woodland, chaparral	Terrestrial (highly petricolous)
S. magister	Semiarid to arid; subtropical thorn scrub, desert-grassland, desert scrub	Terrestrial, with arboreal tendencies (shelters are in the ground)
	(C) *lundelli* subgroup	
S. lundelli	Humid to semi-humid; tropical evergreen forest, tropical deciduous forest, thorn forest	Highly arboreal
S. edwardtaylori	Semi-humid to semiarid; tropical deciduous forest, savanna	Arboreal
S. olivaceus	Semiarid; subtropical thorn forest, live-oak woodland, riparian woodland in subtropical thorn scrub and desert-grassland	Arboreal, with terrestrial tendencies
S. spinosus	Semiarid to arid; subtropical savanna, thorn scrub	Terrestrial, with arboreal tendencies (shelters are in the ground)
S. horridus	Semiarid to arid; subtropical savanna, thorn scrub	Terrestrial, with arboreal tendencies (shelters are in the ground)

1967; Lowe, Cole, and Patton, 1967). The evidence overwhelmingly indicates that the southern, arboreal species of the *spinosus* group that inhabit tropical, humid to semi-humid forests are more primitive than the more northern, semi-arboreal to terrestrial species found in subtropical, semiarid to arid scrub or desert habitats.

Ecological generalizations about the individual species (table 4) reveal that the *melanorhinus* subgroup includes generally southern, relatively arboreal forms that occur in tropical to subtropical forests and woodlands.

Furthermore, there are both southern, arboreal forms that occur in tropical forests, and northern, relatively terrestrial forms that occur in subtropical scrub to desert habitats in the remaining karyotypic subgroups (the *orcutti* subgroup and the *lundelli* subgroup), strongly supporting the recognition of several phylads as suggested above.

Furthermore, the geographic distributions of these nine species are also suggestive. The two species of the *melanorhinus* subgroup (*S. melanorhinus* and *S. clarki*) have contiguous distributions primarily along the Pacific lowlands of Mexico northward to the southwestern United States; *S. melanorhinus* occurs primarily in tropical deciduous forest (fig. 12), as does *S. clarki* in the southern part of its range, but *clarki* also abounds in more xeric-adapted vegetative communities to the north. The species of the *orcutti* subgroup (*S. orcutti* and *S. magister*) have contiguous and largely overlapping distributions in the southwestern United States and northwestern Mexico (including Baja California), with *magister* primarily in the relatively recently derived desert communities (fig. 13) and *orcutti* in the woodlands and at the desert edge. The five species of the *lundelli* subgroup have largely contiguous distributions primarily more to the east of those of the other two subgroups; the relatively arboreal *S. lundelli* occurs largely in the tropical forests on the Yucatan Peninsula; *S. edwardtaylori* is in less humid forests and savannas primarily on the southern portion of the Isthmus of Tehuantepec (fig. 14); *S. olivaceus* occurs in woodland, thorn forest, and thorn scrub in northeastern Mexico and Texas; and the more xeric territory between the ranges of *S. edwardtaylori* and *S. olivaceus* is occupied by the relatively terrestrial *S. spinosus* and *S. horridus* (fig. 15).

Phylogenetic Relationships

My interpretation of the specific relationships within this group is presented in a phylogenetic tree (fig. 16), which I hope is non-deciduous. Inappropriate as it may appear, I followed the classical procedure of illustrating the most derived species at the upper reaches of the branches, although this schematically situates the relatively terrestrial forms in the phylogenetic treetops and the most primitive highly arboreal forms at the base of the tree!

The position of *S. magister* in this phylogeny (fig. 16) may be most readily questioned. *Sceloporus magister,* in overall morphological appearance, seems closely related to *S. horridus* and *S. spinosus;* ecologically and behaviorally it is similar to these species also. I conclude that the similarities result from convergence, as these outwardly similar forms constitute the present terminal (most recently derived) species in their respec-

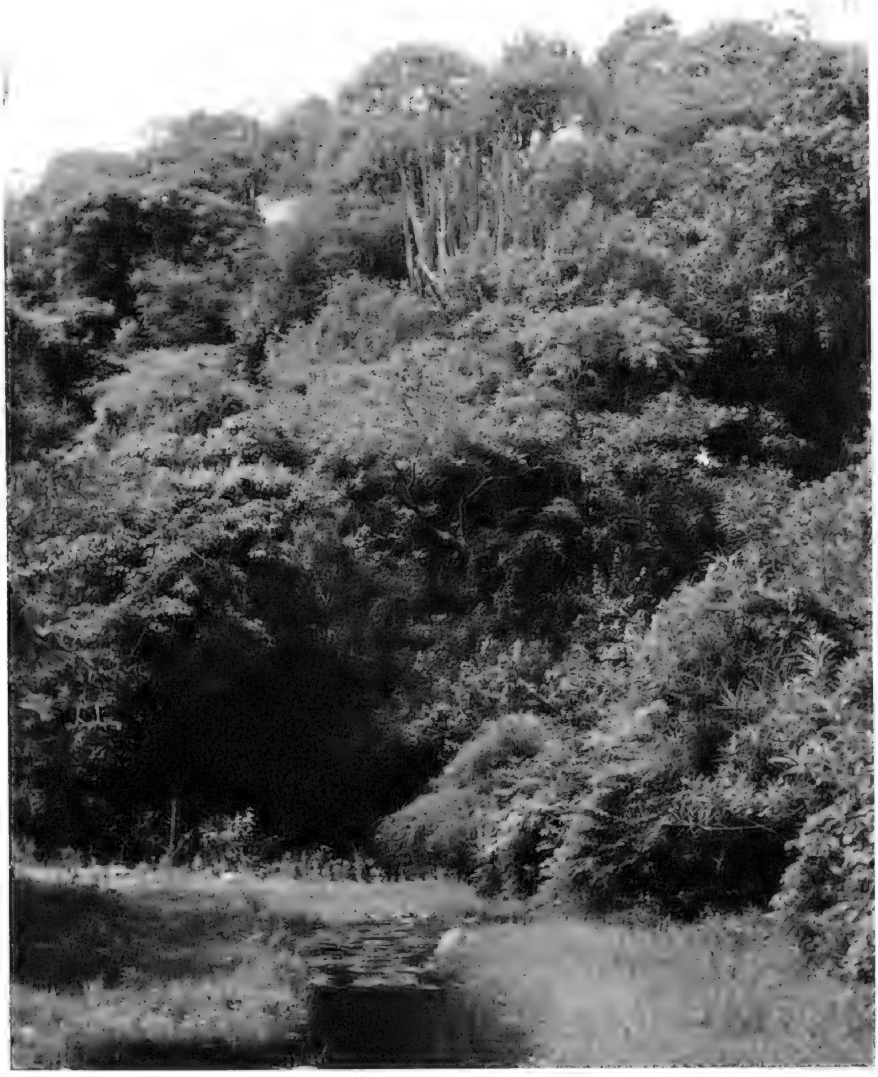

FIG. 12. Riparian tropical deciduous forest in which *Sceloporus melanorhinus* inhabits the largest trees. Two miles (by Mex. 110) east of junction to Colima, Colima, Mexico. Photographed on July 30, 1967.

tive phylads and the trend in each has been adaptive response to increasing aridity and occupation of desert and subdesert communities. In addition to the biogeographic and karyotypic indicators, some details of scutellation are also suggestive of the illustrated relationship (fig. 16); for ex-

FIG. 13. Mohave Desert, inhabited by *Sceloporus magister.* Approximately 5.3 miles east and 4.8 miles south of Llano, Los Angeles County, California, in foothills of San Gabriel Mountains. Photographed by Richard G. Zweifel, December, 1955.

ample, *Sceloporus orcutti* and *S. magister* are the only two species in the entire group in which the first canthal scale is regularly vertically elongated, with the consequence that it is in contact with the lorilabials in nearly all specimens.

Smith (1939, p. 59) presented a phylogeny of the *spinosus* group in his taxonomic monograph, without specifically discussing the criteria on which it was based. While our proposed phylogenies differ significantly, there are some striking similarities. Without explanatory discussion, Smith generally recognized the more tropical and more arboreal forms as relatively primitive in the phylogeny compared with the more terrestrial forms.

Smith considered *Sceloporus magister* as a derivative of the same stock

FIG. 14. Riparian woodland in which *Sceloporus edwardtaylori* inhabits trees; *S. melanorhinus* occupies larger trees in tropical deciduous forest visible on adjacent hills. Seven miles (by Mex. 190) northwest of Tehuantepec, Oaxaca, Mexico, at base of Cerro Quiengola. Photographed on August 21, 1967.

giving rise to *S. horridus, S. olivaceus,* and *S. spinosus,* with the last three species being the most recently derived. This particular relationship is one that might likely be suggested by those who infer phylogenetic relationships solely on the basis of karyotypic information (see above). Some strictly cytogenetically oriented investigators probably would envision one phylad beginning with a *melanorhinus*-type of chromosomal constitution ($2n = 40$, with mostly telocentrics), evolution by means of centric fusion progressively through the northern relatively terrestrial *orcutti*- and *magister*-types, and continuation of this fusion trend directly on to *S. horridus* or *S. spinosus* ($2n = 22$, with mostly metacentrics) in the same phylad; this would require, because of the karyotypic similarities, following through in a geographic circle to the southern, relatively arboreal *S. edwardtaylori* and *S. lundelli* as the most recently derived forms, which

FIG. 15. Tehuacan Desert, inhabited by *Sceloporus horridus*. Seven miles (by road) northwest of Teotitlán del Camino (Oaxaca), in Puebla, Mexico. Photographed on August 12, 1967.

is morphologically, ecologically, and biogeographically unlikely.

The majority of the speciation in the *spinosus* group presumably occurred in the upper middle to late Tertiary Period, particularly in association with the elevation of mountains and plateaus, generally increasing aridity, and the restriction and evolution of vegetative communities (see paleobotanical and herpetological references cited above). The dates involved with this evolution cannot be hypothesized in detail, however, since the Tertiary and Quaternary history of Mexico would have to be known in unreasonably intimate detail in order to be correlated accurately with speciation within such a species group. Nevertheless, the Miocene and Pliocene epochs are attractive as the general time span encompassing most of the speciation in this group, considering in particular the paleobotanical information presented by Axelrod (1948, 1950a, 1950b, 1958, 1960), the paleoherpetological information presented by Tihen (1964), and the present distributions, habitat preferences, and behaviors exhibited by the extant forms. Thus, speciation within the *spinosus* group

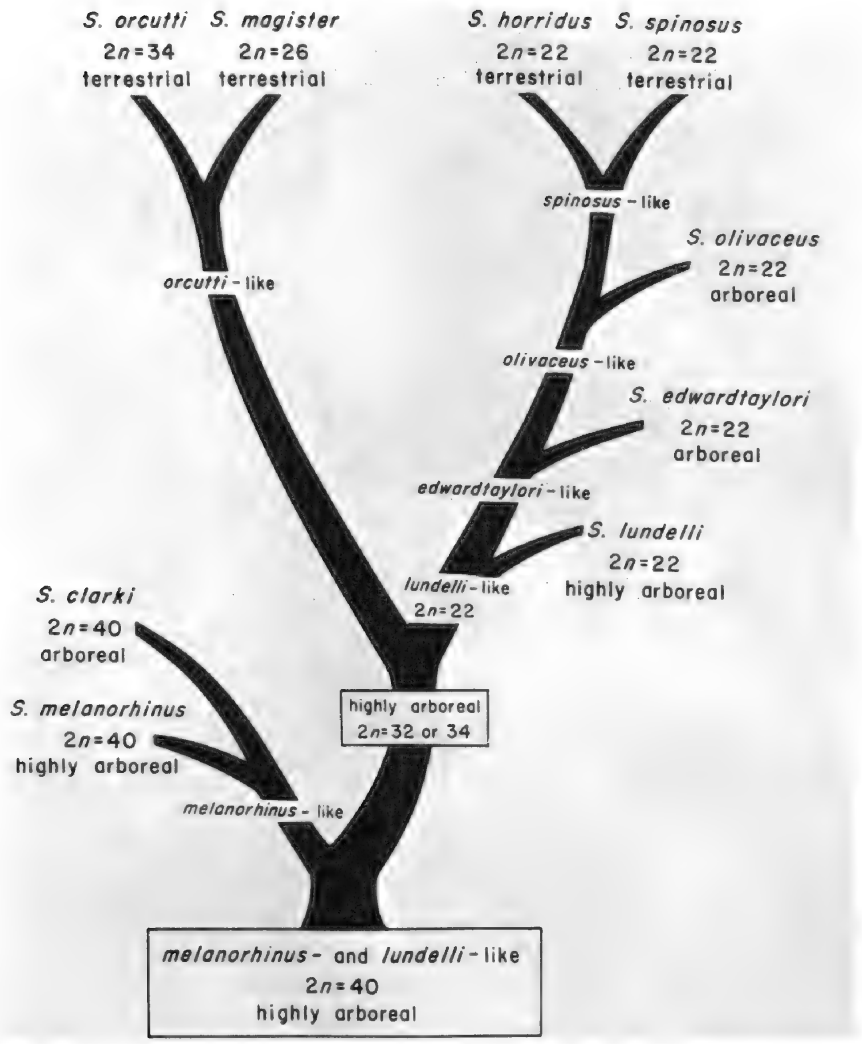

FIG. 16. Proposed phylogeny of the *spinosus* group of lizards in the genus *Sceloporus* (see text).

appears to have involved faunal restrictions as well as derivation *in situ* approximately as described below.

The prototype was a relatively highly arboreal form occupying widespread portions of the Neotropical-Tertiary Geoflora and the newer Madro-Tertiary Geoflora in the Miocene. These lizards had a karyotype essentially identical to the $2n = 40$ karyotype (KA; 20 macrochromosomes+

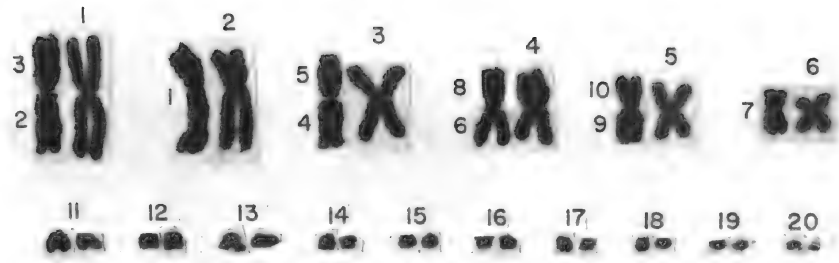

FIG. 17. Composite mock-up "karyotype" representing that of *spinosus* group lizards from hypothetical population ancestral to both the *orcutti* subgroup and *lundelli* subgroup (see fig. 16). This illustrates diploid number of 32; if hypothetical ancestor had $2n = 34$ chromosomes, additional pair would have been microchromosomes as in *S. orcutti,* which has 11 pairs instead of 10 (fig. 5). For macrochromosomes, haploid complements of *S. melanorhinus* [$n = 20$; left chromosome(s) of each "pair"] and *S. lundelli* ($n = 11$; right chromosome of each "pair") have been arranged to illustrate how four centric fusions of particular telocentric macrochromosomes of *S. melanorhinus* could produce metacentric macrochromosomes typical of *S. lundelli* and species in the *lundelli* subgroup. Microchromosomes illustrated here are from the *S. melanorhinus.* Chromosomes of *S. melanorhinus* are from the cell illustrated in figure 4A; those of *S. lundelli* are from the cell illustrated in figure 6B.

20 microchromosomes) occurring in *S. melanorhinus* and *S. clarki* today.

The prototype became isolated (probably geographically rather than ecologically) into two populations; one of these constituted the ancestor of the western *melanorhinus* subgroup, and the other constituted the common ancestor of both the *orcutti* and *lundelli* subgroups (fig. 16). Although the initial isolation was not accompanied by very different ecological adaptations, the karyotype of the western population experienced relatively little or no alteration, while that of the eastern population evolved into the hypothetical $2n = 32$ or 34 condition that is indicated in figure 17. This karyotypic evolution involved four centric fusions (whole-arm translocations) among the macrochromosomes, as illustrated. Since the majority of the more derived species (those in the *lundelli* subgroup) have all macrochromosomes metacentric excepting numbers 2 and 6, which appear to be essentially unchanged from numbers 1 and 7 of the primitive forms, it is likely that the hypothetical fusions produced metacentrics, as illustrated (fig. 17). Note also that this hypothetical karyotype is very similar to that possessed by *S. orcutti* today (fig. 5A).

Not long thereafter, the first divergence near the base of each phylad occurred in response to increased aridity such that the western phylad included populations represented by *S. melanorhinus* (or a direct ancestor

thereto) and *S. clarki* (or a direct ancestor thereto), and the eastern phylad diverged into an *S. lundelli*-like form and an *S. orcutti*-like form. The primitive form of each phylad (*S. melanorhinus* and *S. lundelli*-like) was associated with the older more humid to semi-humid tropical forests, while the newly derived form of each phylad (*S. clarki*-like and *S. orcutti*-like) was associated with the newer semi-humid to semiarid subtropical forests and woodlands. This was not accompanied by extensive karyotypic alterations in the westernmost populations (*melanorhinus* subgroup). In the easternmost populations (*lundelli*-like), however, at least 5 centric fusions among the microchromosomes resulted in the $2n = 22$ condition that characterizes the species in the *lundelli* subgroup today. Meanwhile, in the *orcutti*-like form, the occurrence and fixation of an unequal pericentric inversion in chromosome number 4 resulted in that chromosome being similarly submetacentric in both *S. orcutti* and *S. magister* today (fig. 5).

Further diversification occurred later; in the east, the *lundelli*-like stock diverged into *S. lundelli* and an *edwardtaylori*-like stock, the latter of which subsequently diverged into *S. edwardtaylori* and an *olivaceus*-like stock. The more newly derived forms associated with the relatively drier habitats, with the *olivaceus*-like stock occurring in subtropical woodlands, savanna, thorn forest, and thorn scrub. This divergence in the eastern phylad did not involve extensive karyotypic modifications.

The remaining specific diversification still resulted from the trend toward increased aridity. General southward restriction of the more mesic, ancestral tropical forests was accompanied by southward restriction of the associated ancestral lizards (e.g., *S. melanorhinus* and *S. lundelli*). Meanwhile, in the eastern phylad, the *olivaceus*-like stock diverged into *Sceloporus olivaceus* and a *spinosus*-like stock. The former remained with the semiarid subtropical woodland, thorn forest, and riparian communities to the north and east as they were displaced from the Mexican Plateau by the developing semiarid to arid desert scrub in which the newly derived *spinosus*-like stock developed; shortly thereafter it diverged into *S. spinosus* (to the east) and *S. horridus* (to the west), without involving extensive karyotypic alterations. By now, the more ancestral and arboreal *Sceloporus edwardtaylori* and *S. olivaceus* were geographically separated, due to the interstitial development of more arid-adapted vegetative communities and their associated lizards.

Meanwhile, the *orcutti*-like stock of the western phylad diverged into *S. orcutti* and *S. magister,* also in response to increasing aridity. *Sceloporus magister,* which probably evolved in the Sonoran Desert while *S. orcutti* was restricted to California and Baja California, has become most highly

adapted to the desert environment. This divergence was accompanied by karyotypic evolution including three centric fusions among the microchromosomes in the populations directly ancestral to *Sceloporus magister,* thus resulting in both its lower chromosome number and its possession of some small and clearly bi-armed chromosomes that are somewhat larger than microchromosomes (e.g., pairs 7–9 in *S. magister;* fig. 5B). Also, two inversions are suggested by the different centromere positions in chromosome numbers 1 and 3. The former is metacentric in *S. orcutti* and submetacentric in *S. magister,* while the latter is submetacentric in *S. orcutti* and metacentric in *S. magister* (fig. 5). Since the hypothetical ancestor presumably had these macrochromosomes metacentric (see above; fig. 17), the inversion on chromosome number 1 occurred in the ancestral *magister* population while that on number 3 occurred in the ancestral *orcutti* population, and these inversions occurred following or associated with their divergence. Revelation of the karyotype of *S. orcutti* as representative of an evolutionary intermediate between that of *S. clarki* and that of *S. magister* has resulted in modification of the hypothesized detailed macrochromosome arm homologies of *S. clarki* and *S. magister* as presented by Lowe, Cole, and Patton (1967; compare their fig. 2 with the present fig. 17). It is noteworthy also that those authors apparently correctly hypothesized the occurrence of a pericentric inversion in chromosome number 1 of the ancestral *magister* population following centric fusion of the chromosomes from which it was derived.

Subspeciation and establishment of present geographic ranges of the species in the *spinosus* group probably were the important events of Pleistocene to Recent time. In this regard, it is noteworthy that the more arid-adapted, generally more northern, most recently derived forms in each subgroup are those having the greatest number of subspecies for their respective phylads, revealing their most recent intraspecific evolutionary experimentation and diversification.

SUMMARY

Karyotypes of all the species in the *spinosus* group of lizards of the genus *Sceloporus* were analyzed by means of the colchicine, hypotonic citrate, air-dried technique, employing both bone marrow and testicular tissues. The following cytogenetic phenomena were found within this species group: interspecific and intraspecific variation in chromosome number and morphology; polymorphism in local populations; cytologically recognizable sex chromosomes; and natural chromosomal aberrations.

There are four general karyotypes in the species group, though some

exhibit relatively minor variations. Diploid chromosome numbers range from a high of 40 (with nearly all chromosomes telocentric) to a low of 22 (with all or nearly all chromosomes metacentric or submetacentric). The cytogenetic data, together with ecological, behavioral, and biogeographic data, indicate that speciation within the group has produced several phylads. Karyotypic evolution primarily involved chromosomal centric fusion (whole-arm translocation). The proposed phylogeny of the group is strongly compatible with the evidence that desert-dwelling species were derived from ancestors occurring in tropical to subtropical forests.

SPECIMENS EXAMINED

All specimens (N = 159) from which chromosomes were examined are catalogued individually in the herpetological collection of the Department of Biological Sciences at the University of Arizona (U.A.Z.; catalogue numbers in parentheses).

Sceloporus clarki (N = 81; 46 males, 35 females): Mexico: Sinaloa: 5 miles (by Mex. 15) southeast of Rosario (28305, 28307); 6 miles northwest of La Concha, 29 miles (by Mex. 15) southeast of Escuinapa (28308, 28309); 1 mile northwest of El Aguaje, 13 miles (by Mex. 15) northwest of Río Elota (28310, 28311). Sonora: Alamos (25685); abandoned tequila factory, 2 miles west of Alamos (16237, 16238); 7.5 miles (by Alamos Road) west of Alamos (25466, 25472); La Aduana Watermine, *ca.* ½ mile north of La Aduana (24211); along Río Mayo, Navojoa (18127, 16221–16223, 25467, 25686–25688, 25690, and 25691). United States: Arizona: Coconino County: Verde Valley School, *ca.* 7 miles south of Sedona (21860). Pima County: Kitt Peak, Quinlan Mountains (16228); Sycamore Canyon, *ca.* 3700 feet elevation, Baboquivari Mountains (24222); Milagrosa Canyon, *ca.* 3000 feet elevation, (16239). Santa Cruz County: Sycamore Canyon, 3800 feet elevation, Pajarito Mountains (24186, 24195, 24206, 24207, 24209, 24214, 24218, 24862–24867, 24869, 24870, 24872, 24873, 24876, 24878–24880, 24883, 24885, 24904, 24906, 25456, 25458, 25461, 25464, 25469, 25470, and 25473); either Sycamore Canyon, *ca.* 3800 feet elevation or 13.1 miles (by Ruby Road) west of U.S. 89, in vicinity of West Peña Blanca Canyon, 4200 feet elevation, Pajarito Mountains (25465, 25468, and 25471); White Oak Mine, Walker Canyon, 1.9 miles (by road) southwest of 7.7 miles (by Ruby Road) west of Nogales Highway, *ca.* 4200 feet elevation, Pajarito Mountains (19082); Walker Canyon, *ca.* ½ mile (by road) southwest of 7.7 miles (by Ruby Road) west of Nogales Highway, *ca.* 3900 feet elevation, Pajarito Mountains (24874, 25454, 25455, 25457, 25459, 25460, and 25462); vicinity of Peña Blanca Spring, Pajarito Mountains (24187); Sycamore Canyon, *ca.* 7 miles on Washington Camp Road east of junction with Arizona 82, *ca.* 4500 feet elevation, Patagonia Mountains (24871, 24877, 24884, 24887, and 25463); Sycamore Canyon, Patagonia Mountains (24896); Duquesne, 5100 feet elevation, Patagonia Mountains (24875). New Mexico: Catron County: San Francisco (Frisco) Hot Springs, 4800 feet elevation (16218–16220). Grant County: *ca.* 2 miles (by road) south of Pinos Altos (16226).

Sceloporus melanorhinus (N = 7; three males, four females): Mexico: Chiapas: Jardín Botánico, Tuxtla Gutiérrez (28300). Colima: 2 miles (by Mex. 110) east of junction to Colima (28299, 28303, and 28304). Guerrero: vicinity of Villa Treppiedi, Acapulco (18548, 28301, and 28302).

Sceloporus orcutti (N = 8; four males, four females): Mexico: Baja California Sur: Boca de la Sierra (18550). United States: California: Riverside County: *ca.* 9 miles (by California 74) southeast of Hemet, North Fork of San Jacinto Creek, San Jacinto Mountains (21669–21672); 2 miles (by road to Idyllwild) south of Banning, San Jacinto Mountains (21674); 3 miles (by road to Idyllwild) south of Banning, San Jacinto Mountains (21673). San Diego County: California 78 crossing of San Felipe Creek, west of Anza-Borrego Desert State Park (21675).

Sceloporus magister (N = 16; nine males, seven females): Mexico: Sonora: 17.6 miles south of International Border (Lukeville, Pima County, Arizona), on road to Puerto Peñasco (16227); *ca.* 2 miles (by road) north of Desemboque del Río San Ignacio (24197). United States: Arizona: Mohave County: Alamo Crossing (16215, 16216, 16231, and 16232). Pima County: north end of Campbell Avenue, north of Tucson (16225); 3 miles north on Soldier's Trail from Reddington Road, 2800 feet elevation (16235); ¼ mile south of Ajo Road, on Sierra Mountain Road (16234); southeast corner of Anklam and Greasewood, north of Tumamoc Hill, west of Tucson (16236); Tanque Verde Creek, on north edge of Tanque Verde Country Club, northeast of Tucson (16230). Pinal County: 11.9 miles southeast of Mammoth on Mammoth to Reddington Road, at San Pedro River crossing (16229, 16233). Utah: Garfield County: Trachyte Creek, 8.1 miles (by road to Bullfrog) south of Utah 95, 4900 feet elevation, Henry Mountains (16224). San Juan County: Rainbow Bridge National Monument (21859, 21867).

Sceloporus lundelli (N = 13; eight males, five females): Mexico: Yucatan: Pisté (28337, 28345, 28346, 28349, and 28350); Balneario Chicalá, *ca.* 2 kilometers east of Río Lagartos (28339–28344, 28347, and 28348).

Sceloporus edwardtaylori (N = 9; six males, three females): Mexico: Oaxaca: Juchitán (28359 and 28365–28367); Puente Las Tejas, base of Cerro Quiengola, 7 miles (by Mex. 190) northwest of Tehuantepec (28368, 28369, 28371, 28372, and 28376).

Sceloporus olivaceus (N = 12; five males, seven females): United States: Texas: Kendall County: 7 miles (by Interstate 10) northwest of Boerne (28335). Kerr County: Guadalupe River at 8 miles (by Texas 39) south of Camp Mystic (19 miles south of Ingram) (28334). Travis County: Municipal Golf Course (Lake Austin and Exposition Drive), Austin (28326–28333). Val Verde County: 1 mile north of old Devil's River bridge, near Devil's River (24199); Devil's River, near site of old Devil's River bridge (old U.S. 90), northwest of Del Río (24205).

Sceloporus spinosus (N = 5; one male, four females): Mexico: Guanajuato: 3 miles south of Cacalote, 14 miles (by road to Salvatierra) south of Celaya (28353, 28354). Oaxaca: 5 miles (by Mex. 175) northwest of Miahuatlán (28355); 8 miles southeast of El Tule, 13 miles (by Mex. 190) southeast of Oaxaca de Juárez (28351, 28352).

Sceloporus horridus (N = 8; six males, two females): Mexico: Colima: 2 miles (by Mex. 110) south-southwest of junction to Colima (28324); vicinity Tecuizitlán, 8 miles (by Mex. 110) east of junction to Colima (28312). Guerrero: *ca.* 2 kilometers (by Mex. 95) south of junction to Iguala (18119). Jalisco: 1 mile

(by Mex. 80) northeast of Autlán (28319). Nayarit: vicinity El Refugio, 8 miles (by Mex. 15) southeast of Tepic (28315, 28317); 3 miles (by road) northeast of Santa María del Oro (28322). Puebla: 7 miles (by road) northwest of Teotitlán del Camino (Oaxaca) (28321).

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